The Hemiuroidea : terminology, systematics and evolution

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Synopsis

The history of the classification of the Hemiuroidea and the features which have been used as criteria for distinguishing the higher taxa, such as adult morphology, life-cycle patterns and cercarial anatomy, are discussed. It is suggested that the best basic criterion currently available is the functional morphology of the adult.

Explanations of the terminology with comments on the systematic significance and possible function of the features used in the study of hemiuroid taxonomy are included.

A classification of the Hemiuroidea is presented with keys and definitions of the taxa to the generic level. The classification and definitions are based, where possible, on original observations of sectioned material. The Hemiuroidea is divided into fourteen families. The Accacoeliidae contains the Accacoeliinae and Paraccacladiinae, the latter subfamily consisting of only one genus. The Azygiidae consists of two subfamilies, the Azygiinae and Leuceruthrinae. The Bathycotylidae, Isoparorchiidae and Ptychogonimidae contain single genera, while the Hirudinellidae contains three monotypic genera. The Bunocotylidae is

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redefined and contains the Bunocotylinae, Aphanurinae, Opisthadeninae (including *Neotheletrum* gen. nov.) and Theletrinae subfam. nov. The Derogenidae is also redefined and contains the Derogeninae, Gonocercinae and Halipeginae. The hemiuroids from the teleost swim-bladder, with the exception of *Isoparorchis*, are placed in the Dictysarcidae, which is composed of the Dictysarcinae, Albulatrematinae and Cylindrorchiinae subfam. inq. The Hemiuridae is restricted to ecsomate forms and contains the following subfamilies: Hemiurinae, Dinurinae, Elytrophallinae, Glomericirrinae, Hypohepaticolinae, Lecithochiriinae, Lethadeninae, Plerurinae subfam. nov. and Pulmoverminae. The Lecithasteridae is redefined and is composed of the Lecithasterinae, Hysterolecithinae (including *Thulinia* gen. nov.), Macradeninae, Prolecithinae, Quadrifoliovariinae and Trifoliovariinae. The Sclerodistomidae contains the Sclerodistominae, Prosogonotrematinae and Prosorchiinae. The Sclerodistomoididae fam. nov. is erected for *Sclerodistomoides*, and in the Syncoeliidae, the Syncoeliinae and Otiotrematinae are redefined. An index to the generic names used in this classification is included.

The criteria which may be used as indicators of the relative 'primitiveness' of various taxa or to illustrate phylogenetic relationships within the group are discussed. In relation to this, evolutionary trends within three organ-systems, (1) the seminal storage and disposal apparatus in the female reproductive system, (2) the vitellarium and (3) the terminal genitalia, are studied in detail. Using evidence from this study, an evolutionary picture for the Hemiuroidea is presented, and its relationships with the Didymozooidea and the Paramphistomoidea are commented upon.

I. Introduction

The superfamily Hemiuroidea Looss, 1899, is a group within the Digenea which includes species usually parasitic in the gut, particularly in the stomach, of fishes. They are found predominantly in marine teleosts, but also occur in freshwater teleosts, elasmobranchs and occasionally in amphibians and reptiles. It is not unusual for progenetic forms to occur in molluscs and other marine, and occasionally freshwater, invertebrates. In addition to the alimentary canal of fishes, examples are known from the gall-bladder, swim-bladder, body-cavity, mouth, gills and from the skin, whilst all known species of one group are found in the lung of sea-snakes. Overall, the hemiuroids form a very diverse group, not only in habitat, but also in morphology. Indeed, the wide variations in adult morphology, even within proposed higher taxa, have resulted in a good deal of confusion with regard to the validity, composition and systematic relationships of these taxa.

The superfamily was erected, under the name Hemiurida, by Dollfus (1923), and comprised the families Hemiuridae, Accacoeliidae and Syncoeliidae. Prior to this Looss (1907, 1908) had carefully re-described many species of hemiuroids and set a basic pattern on which later authors, notably Odhner (1911), Poche (1926) and Führmann (1928), were able to build. These early workers based their classifications entirely upon adult morphology and divided the group into a small number of families, although not always indicating the relationships between these families. Odhner (1911), for example, grouped three families together, the Hemiuridae, Azygiidae and Didymozoidae. Since Odhner, the concept of the Hemiuridae has been sub-divided, condensed and sub-divided again on numerous occasions. Systematic histories of the Hemiuroidea have been compiled by Chauhan (1954), Skrjabin & Guschanskaja (1954, 1956, 1960) and more recently by Stunkard (1973), although the latter author has omitted the important contributions of Chauhan (1954), Manter & Pritchard (1960a) and Mehra (1962). In order to avoid repetition, we have condensed several of the more recent conceptions of the Hemiuroidea in the form of Table 1. It can be seen from this table that Odhner's original conception was split by Yamaguti (1971) into three superfamilies and eighteen families, one of which, the Hemiuridae, contains twenty-five subfamilies. The large number of higher taxa in this rather uncritical work of Yamaguti appears to be the result of the acceptance of inadequate descriptions as being accurate. Stunkard (1973) summarized the problem succinctly as follows: 'in the course of the past hundred years, a large number of trematodes have been described, many on inadequate and erroneous information and based often on a single specimen. New genera and higher taxonomic categories have been erected to receive these dubious species.' Yamaguti, for example, has accepted three genera in three different families for forms which we consider to be synonymous with the genus *Elongoparorchis* Rao, 1961.

Recent conceptions of the Hemiuroidea, and of the Digenea in general, have been greatly

Table 1 Some recent classifications of the Hemiuroidea

Present classification	La Rue (1957)	Skrjabin & Guschanskaja (1956; 1958; 1960)	Manter & Pritchard (1960a)	Mehra (1962)	Yamaguti (1971)
HEMIUROIDEA Accacoeliidae Azygiidae Bathycotylidae Bunocotylidae Derogenidae Dictysarcidae Hemiuridae Hirudinellidae Isoparorchiidae Lecithasteridae Ptychogonimidae Sclerodistomidae Sclerodistomoididae Syncoeliidae	**Hemiurata** **HEMIUROIDEA** Bathycotylidae Didymozoidae Dinuridae Halipegidae Hemiuridae Isoparorchiidae Lecithasteridae Lecithochiriidae Ptychogonimidae **Azygiata** **AZYGIOIDEA** Azygiidae Bivesiculidae **TRANSVERSOTREMATOIDEA** Transversotrematidae (Some families omitted due to lack of information on life-history)	**Hemiurata (1960)** **HEMIUROIDEA** Accacoeliidae Aerobiotrematidae Bathycotylidae Dinuridae Elytrophallidae Halipegidae Haplosplanchnidae Hemiuridae Isoparorchiidae Lampritrematidae Lecithasteridae Lecithochiriidae Ptychogonimidae Sclerodistomidae Syncoeliidae **Azygiata (1958)** **AZYGIOIDEA*** Azygiidae Hirudinellidae Liocercidae Xenoperidae **? SUPERFAMILY** Aphanhysteridae Botulidae Prosthogonotrematidae	**HEMIUROIDEA** Accacoeliidae Aerobiotrematidae Didymozoidae Hemiuridae Hirudinellidae Isoparorchiidae Prosogonotrematidae Syncoeliidae **'Azygiata'** Azygiidae Ptychogonimidae	**HEMIUROIDEA** Accacoeliidae Arnolidae Bathycotylidae Hemiuridae Hirudinellidae Isoparorchiidae Lampritrematidae Oesophagicolidae Prosogonotrematidae Ptychogonimidae Sclerodistomidae Syncoeliidae (Families not considered to be hemiuroid are not dealt with)	**HEMIUROIDEA** Bathycotylidae Botulidae Hemiuridae Hirudinellidae Lampritrematidae Mabiaramidae Prosogonotrematidae Ptychogonimidae Sclerodistomidae **ACCACOELIOIDEA** Accacoeliidae **ISOPARORCHIOIDEA** Aerobiotrematidae Albulatrematidae Cylindrorchiidae Dictysarcidae Isoparorchiidae Pelorohelminthidae Tetrasteridae **? SUPERFAMILY** Azygiidae ? Aphanhysteridae Syncoeliidae (related to Hemiuridae)

* 1956 – included in Hemiurata.

influenced by the work of La Rue (1957), who sub-divided the Digenea into two groups, the Epitheliocystidia and the Anepitheliocystidia, depending upon the epithelial or membranous nature of the lining of the cercarial excretory vesicle. The Azygiidae was placed in the latter group, while the remainder of the hemiuroids with 'known' life-histories were placed in the former. This work has resulted in the majority of recent workers considering the Azygiidae to be distinct from the Hemiuroidea, at least at the superfamily level (see Odening, 1974). Work by Powell (1972, 1973, 1975) and Gibson (1974) indicated that it is likely that all cercariae have a syncytial lining to the excretory vesicle. This casts grave doubts upon the validity of La Rue's conceptions.

Yamaguti (1971) stated that life-cycle patterns may be an important systematic feature; but, due to a lack of knowledge with regard to the life-histories of this group, this aspect appears to be of little use in its classification. The little that is known suggests that, even within one family, the life-cycle can vary considerably in detail (see Chabaud & Buttner, 1959; Sinclair *et al.*, 1973; Bray & Gibson, 1977). Stunkard (1973) gave a useful four-page summary of the present knowledge of the hemiuroid life-cycle, and Yamaguti (1975) lists much of this information in more detail. Stunkard introduced his contribution as follows: 'The wide divergence of opinion concerning the systematics and classification of the hemiuroid trematodes is the result, in large measures, of lack of knowledge of their life-cycles and developmental stages. Data are meager, fragmentary, often faulty, and sometimes erroneous.' He summarized his findings thus: 'The miracidia of the hemiuroid, azygiid and didymozoid species are unique and very similar. All are aciliate, provided with an anterior circle of spines, and the surface of the body bears bristles . . . The cercariae develop in rediae; they lack penetration and cystogenous glands, and develop into the cysto-phorous stage which is characteristic for hemiurid trematodes. Typically they are eaten by copepods and the metacercariae occur as unencysted larvae in the hemocoel of the crustaceans or other planktonic invertebrates that feed on copepods . . . The striking similarity of the larval stages, and the fact that they are peculiar to the hemiurid trematodes, portends genetic homo-geneity and despite adult adaptations to different situations, the thesis of Odhner and Führmann that the Azygiidae, Hemiuridae and Didymozoidae are closely related is probably correct'. We agree that these groups do seem to be closely related, although we are reluctant to place too much emphasis on larval stages, especially considering the recent work of Devaraj (1972) and Schell (1975), who have described ciliated, non-spinous miracidia for the hemiuroids *Isoparorchis hypselobagri* (Billet, 1898) and *Lecithaster salmonis* Yamaguti, 1934, respectively. Similarly, a small number of cystophorus cercaria such as, *Cercaria vaullegeardi* Pelseneer, 1906, are known to develop in daughter-sporocysts and not rediae (see Popiel, 1976). We are not convinced of the primitive nature of the cercaria relative to the adult, because of the morphological similarities between what we consider to be primitive hemiuroids and the aspidogastreans (see below). The hypothesis that the present adult digenean evolved from a mature, free-swimming cercaria-like adult is presented by Cable (1965, 1974). It appears more likely to us that the adult forms from vertebrates arose directly from primitive molluscan parasites, in much the same way as many aspi-dogastreans, and that the crustacean host and the cercarial stage are more recent developments. Pearson (1972) and Rohde (1972) discuss the two contrasting hypotheses concerning the evolu-tionary significance of the digenean life-cycle. It seems likely that the morphological differences in cercariae, hitherto used as systematic indicators, are, at least to some extent, the result of the ecological requirements of the life-history. If, for example, the crustacean host is benthic, then the cercarial tail will tend to be of a different shape to that of a species which has a pelagic crusta-cean host. In other superfamilies, such as the Allocreadioidea, there appear to be major differences in the cercariae of different families. A similar argument also applies when considering the chaetotaxy of cercariae as a systematic criterion. In the latter case there is no reason why the hypertrophy or atrophy of the nervous system does not depend upon the ecological requirements of the life-history. One additional disadvantage in using larval characteristics or life-history for systematic purposes, is that for the majority of determinations only adult-specimens are available for study. The lack of knowledge with regard to the larval stages and life-histories of the great majority of genera, however, remains the greatest limitation to their value in systematics. We suggest, therefore, that the use of life-history details, and particularly cercarial morphology, should be treated with *at least* as much caution as the use of adult morphology.

We consider that neither the gross morphology of the adult, due to its variability, nor the use of life-cycle patterns and cercarial morphology, due to a lack of knowledge and understanding with regard to their significance, are able to provide us with a satisfactory classification. In our opinion, functional morphology appears to offer the best alternative. In order to use this concept, one must have a detailed knowledge of the morphology of an organ or organ-system and an understanding of its probable function. Once its function is understood, one can then comprehend the requirements for such an organ in order that the animal might complete its life-history. With an understanding of the function and requirement for particular organs and organ-systems, one can rationalize many of the diverse variations which occur in different taxa, and recognize where development or atrophy has occurred. This sheds light, not only upon the systematics, but also upon the phylogenetic relationships of the taxa. It also tends to expose inaccurate descriptions and is a useful aid in suggesting the probable structure of particular organs in inadequately described taxa. The following classification, which we propose for the Hemiuroidea, is based, therefore, upon adult morphology associated with an attempted understanding of the function of organs and organ-systems. This functional aspect has permitted us to try and base our concepts upon a combination of features, rather than upon one critical feature.

II. Definitions of hemiuroid structures* with comments on their systematic value and possible function

Accessory excretory organ (*vesicle*) – see *Manter's organ*.

Annulations or *annular plications* – see *plications*.

Blind seminal receptacle – a type of seminal receptacle which does not communicate with the exterior via Laurer's canal, but which is linked to the oviduct by a short duct (Fig. 1) and usually has a thick wall. It serves as a seminal store, and its presence, except in the cases in the Trifoliovariinae and Derogeninae where it appears to have arisen from a canalicular seminal receptacle by the loss of Laurer's canal, appears to be a good systematic feature at the subfamily level. It is worth noting that when a blind seminal receptacle is present, the uterine seminal receptacle (q.v.) is lost. See *seminal receptacle*.
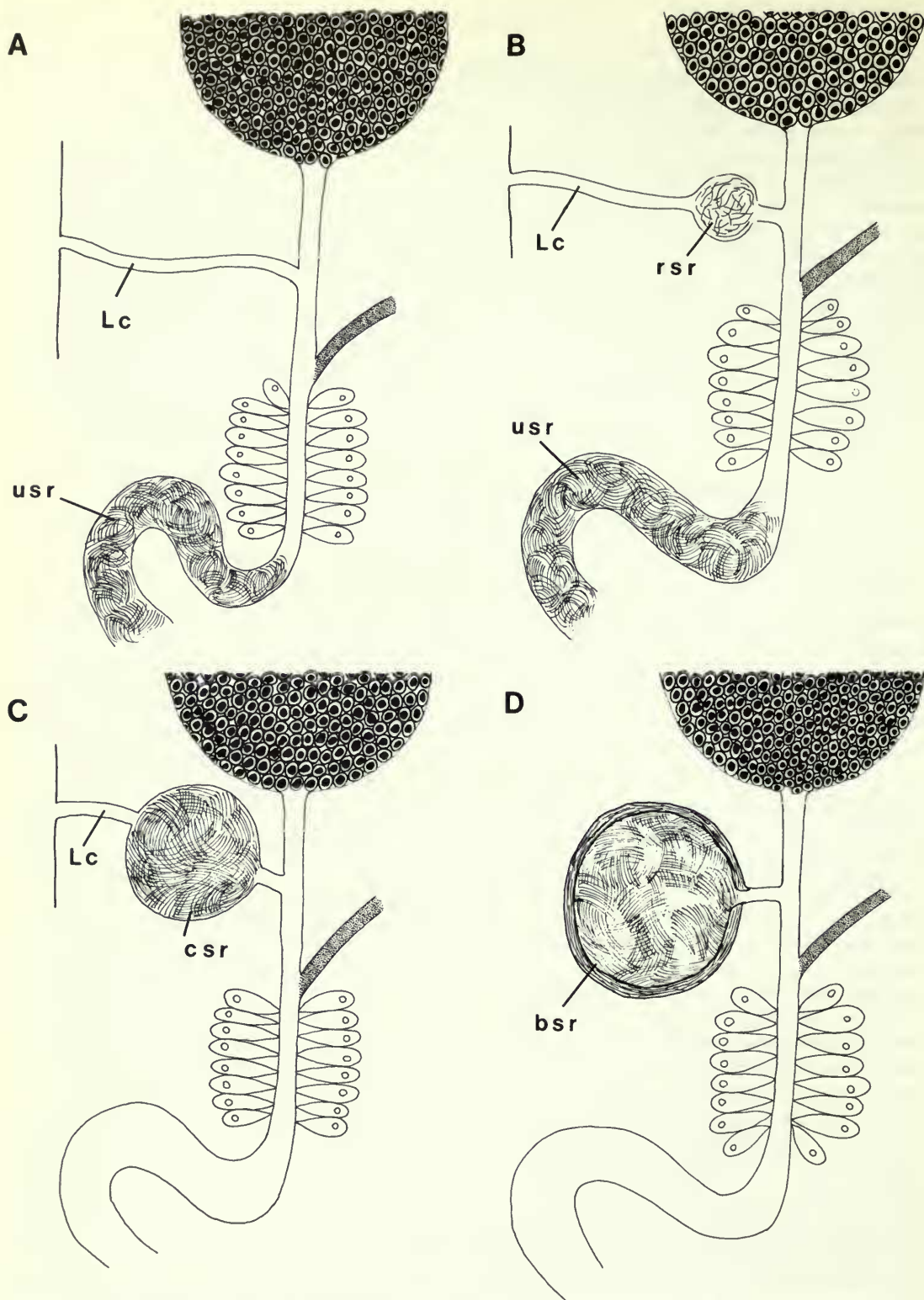
Canalicular seminal receptacle – a large proximal dilation of Laurer's canal which is normally filled with fresh, as opposed to spent, spermatozoa (Fig. 1). This type of seminal receptacle (q.v.) in the majority of cases is possibly a recent adaptation associated with the use of Laurer's canal as a vagina (Gibson & Bray, 1975). See *seminal receptacle*.

Cirrus – an intromittent copulatory organ which is formed from or encloses the male duct only. It is rare in hemiuroids, occurring only in the members of the Hirudinellidae. Although its presence in certain other hemiuroid groups has been indicated in the literature, in two such cases, the hemiurid *Glomericirrus* and the derogenid *Arnola*, our observations of sectioned material show that this structure is definitely absent, there being a sinus-organ (q.v.) present. The occurrence of a cirrus in the Hemiuroidea, therefore, is most likely a feature of importance at the family level. It is unlikely, however, that the 'cirrus' of the hirudinellids is homologous with the cirrus common in many groups of Digenea.

Cirrus sac – a muscular sac which surrounds the terminal portion of the male duct including the cirrus. Its function appears to aid the eversion of the cirrus (q.v.) and the expulsion of spermatozoa, as it often encloses the seminal vesicle (q.v.), during copulation by exerting hydrostatic pressure upon its contents. It is to some extent, therefore, analogous with the sinus-sac (q.v.). This structure occurs in the Hirudinellidae: its reported presence in other hemiuroid groups, such as the Halipeginae, we consider to be extremely doubtful. The presence of a cirrus-sac is in our opinion a feature of importance at the family level in the Hemiuroidea.

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* It should be noted that a smaller glossary of terms used in hemiuroid systematics was produced by Manter (1970). There are, however, significant differences between some of our definitions and those of Manter.

Fig. 1. The different types of seminal receptacle present in the Hemiuroidea: A. Uterine seminal receptacle; B. Rudimentary seminal receptacle; C. Canalicular seminal receptacle; D. Blind seminal receptacle. [bsr, blind seminal receptacle; csr, canalicular seminal receptacle; Lc, Laurer's canal; rsr, rudimentary seminal receptacle; usr, uterine seminal receptacle.]

Cyclocoel – the name given to the gut-caeca when fused terminally, thus forming a complete caecal ring. The advantage of this caecal arrangement is unknown. This feature is of generic importance only, as it occurs widely in unrelated groups both within and outside the Hemiuroidea. The apparent cyclocoel found in large specimens of *Hirudinella* appears to be a subterminal fusion of the gut-caeca which takes place during the development of the animal.

'*Drüsenmagen*' – this structure, the name of which means 'glandular stomach', is found at the 'shoulder'-region of the gut-caeca in many hemiuroids. It is usually an expanded region lined by large, glandular cells forming a villous luminal surface, which is readily distinguished from the lining of the remainder of the caecum. Its function is not known, but it is probably a region of specialized secretion and/or digestion. It does not appear to be of systematic significance as it occurs widely in distantly related hemiuroids, but it is apparently absent in the azygiids. Manter (1970) refers to these structures as 'precaecal sacs'.

Ecsoma – this is the name given to the posterior region of the body of an adult digenean, when it is capable of being retracted within the body (soma). This structure, which appears to be unique to the Hemiuridae, is occasionally referred to as a 'tail' or the specimens are referred to as 'appendiculate' or 'ecsomate'. The gut-caeca, uterus and, on rare occasions, the ovary and vitellarium may extend into the ecsoma, and the excretory pore opens terminally on it. The mechanism of extension is not known, although the body-wall clearly contains longitudinal and circular muscles; but within the ecsoma are numerous large, vesicular cells which might be involved with this process, acting as a hydrostatic skeleton. Its function is thought to be that of a feeding organ which is extruded during periods when the pH or the osmolarity of the stomach contents is at a tolerable level. It should be noted that hemiurids tend to occur in the lumen of the stomach, especially the pyloric region, of marine teleosts and are, therefore, subject to great variations in pH and osmolarity (MacKenzie & Gibson, 1970). We suggest that other groups present in the stomach of these fish, such as the derogenines, tend to live more in the cardiac end of the stomach and only migrate down into the lumen during periods of more neutral pH and/or low osmolarity. These suggestions are made on the basis of observations of *Derogenes varicus* and *Hemiurus communis*. In relation to this function, the development of the ecsoma appears to be associated with the development of plications (q.v.) of the tegument.

As the ecsoma occurs only in the hemiurids, this feature is of importance at the family level. In some groups, however, such as in some of the lecithochiriine genera, the ecsoma may be reduced in size.

Egg-filaments – in a few hemiuroids the egg-shell may be drawn out at the poles to form filaments. Usually, these are unipolar and may be of variable length. Occasionally, they are bipolar and may bear more than one filament (e.g. *Anguillotrema*). It is likely that these filaments are part of a mechanism associated with the acquisition of the first intermediate host. They may, for example, become attached to the gill-filaments of the mollusc. In the case of *Hypohepaticola*, which tends to be a tissue-parasite, the spine-like filament may aid the exit of the egg from the tissue by a mechanism similar to that found in schistosomes. The presence of egg-filaments is a feature of only generic importance, as it occurs spasmodically throughout the group, particularly in the Derogenidae.

Ejaculatory duct – the entire male duct distal to the seminal vesicle can theoretically be referred to as the ejaculatory duct. Regions such as the pars prostatica (q.v.) and cirrus (q.v.) are modifications of the ejaculatory duct. In the hemiuroids, however, the region generally referred to as the ejaculatory duct is an unmodified region of this duct and is, therefore, without an alternative name. When present, it occurs between the pars prostatica and the hermaphroditic duct (q.v.) [or terminus of the male system]. It may occur entirely or partly inside or outside the sinus-sac (q.v.). This region of the duct is of little systematic importance, except perhaps at the specific level; but it is long in certain lecithasterids, especially in the Macradenininae. Occasionally, unmodified regions of the male duct occur between the seminal vesicle and the pars prostatica or separating two regions of the pars prostatica. These regions, however, are not referred to as the ejaculatory duct, but usually as tubular extensions of the seminal vesicle or aglandular regions of the pars prostatica.

Ejaculatory vesicle – a dilation of the ejaculatory duct (q.v.) within the sinus-sac (q.v.). This feature occurs in certain lecithochiriine genera and, in its glandular form (see *prostatic vesicle*), in the Glomericirrinae, Hysterolecithinae and the remainder of the lecithochiriines. It appears to function as a small seminal reservoir as part of a mechanism to increase the amount of spermatozoa ejected from the sinus-sac during copulation. Nasir & Diaz (1971) suggest that an ejaculatory vesicle is merely a prostatic vesicle from which the cellular lining has been lost, hence we suggest that it might be more appropriate to refer to the prostatic vesicle as a 'glandular ejaculatory vesicle' (see p. 93). The presence of an ejaculatory vesicle or a glandular ejaculatory vesicle (prostatic vesicle) is a feature of importance at the subfamily level.

Excretory vesicle (*bladder*) – in hemiuroids this is essentially Y-shaped, the arms often uniting dorsally to the pharynx or oral sucker. The presence of blind arms is a feature of no more than generic importance, as it appears to occur widely in distantly related forms, and indeed we have not used it at the generic level in the case of the azygiid genus *Otodistomum*. There are a number of modifications of the basic structure of this organ, especially in the stouter hemiuroids. These include: (1) in the Sclerodistomidae there are one or two Manter's organs (q.v.), often called 'accessory excretory vesicles', which communicate with this organ distally; (2) in *Hirudinella*, *Botulus* and *Sclerodistomum* the arms form a branching system of tubules or diverticula; (3) in some of the primitive groups, such as the Accacoeliidae, Hirudinellidae and Syncoeliidae, the excretory arms are usually arranged so that initially they pass forward dorsally and ventrally, instead of laterally; and (4) in the Ptychogonimidae the excretory arms unite twice in the forebody.

Fischthal's organ – this is a name given by Yamaguti (1971) for a round vesicle of unknown function, lined with epithelial cells and surrounded by a dense mass of gland-cells, which apparently opens dorsally to the right of Mehlis' gland (q.v.) in *Pelorohelmins palawanensis* Fischthal & Kuntz, 1964. There is no evidence of such a structure in specimens under the name of *P. ghanensis* Fischthal & Thomas, 1968, from the collection of the British Museum (Natural History). It is possible, therefore, that Yamaguti may have mistaken Juel's organ (q.v.) for this structure. He also, however, describes this structure in *Meristocotyle varani* Fischthal & Kuntz, 1964, a species of unknown relationship; but in this case it is the distal dilation of Laurer's canal which opens dorsally. [We should point out that we regard *Pelorohelmins* to be a synonym of *Elongoparorchis*.]

Genital atrium – a receptacle present in most hemiuroids between the hermaphroditic duct and the genital pore, which probably acts as a vagina during copulation. Spermatozoa are probably deposited within this structure by the copulatory organ of another worm when cross-insemination occurs, and it is then either sucked back into the hermaphroditic duct by the action of the sinus-sac or, more likely, forced back (the sinus-organ being retracted to receive it) by the action of the muscular walls of the genital atrium which are contractile. The lining of the genital atrium is continuous with the sinus-organ (or in the case of the hirudinellids, the 'cirrus'), and appears to contribute significantly to the formation of its outer surface as it extends. In some of the hirudinellids the genital atrium may be everted through the genital pore, thus giving extra length to the 'cirrus' (see Fig. 12D of Gibson & Bray, 1977). This also occurs in *Isoparorchis* (Fig. 2), where it adds additional length to the sinus-organ.

The contractile nature of this organ makes it of limited taxonomic value, even at the specific level, although its apparent total absence may be of some value. It is often reduced or absent in species which must rely upon self-insemination or which possess only a temporary sinus-organ. When the sinus-organ and sinus-sac are absent, it is difficult to distinguish the genital atrium from the hermaphroditic duct. In such cases, these two terms often appear to have been used interchangeably.

Genital pore – the aperture through which the contents of the genital ducts pass to the exterior. It usually, in the Hemiuroidea, forms the mouth of the genital atrium, but occasionally occurs at the distal end of the hermaphroditic duct, when the genital atrium (q.v.) is absent, or at the union of the male and female ducts when both the hermaphroditic duct and the genital atrium are absent. The genital pore is not always the most distal part of the terminal genital apparatus, as during copulation the copulatory organ, or even the genital atrium, is thrust through the genital
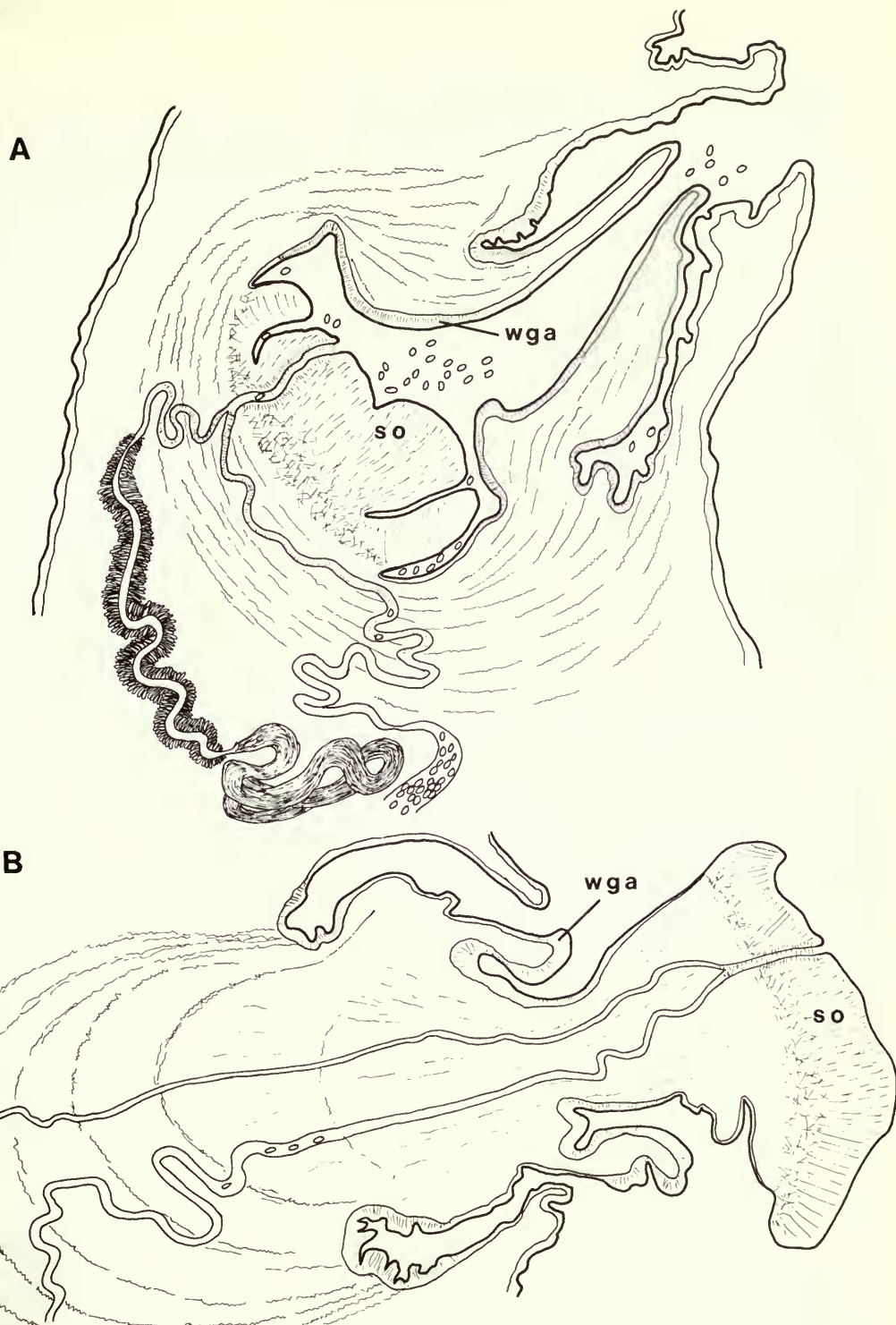
Fig. 2 Sagittal sections through the terminal genitalia of *Isoparorchis*: A. Withdrawn; B. Extruded. [so, sinus-organ; wga, wall of genital atrium.]

pore. This structure is of little systematic importance as it occurs mid-ventrally in the anterior forebody in all hemiuroids.

Hermaphroditic duct – a duct commonly linking the terminal male and female ducts with the genital atrium. The duct itself appears to have arisen partly as a modification of the genital atrium and partly from the fusion of the male and female ducts. It is normally quite distinct from the genital atrium; but, in certain cases, when the sinus-sac and sinus-organ are absent, it is difficult to distinguish these structures. An hermaphroditic duct occurs in most hemiuroids, commonly within the sinus-sac and almost always within the sinus-organ, when the latter structure is present. Annular muscles are sometimes clearly seen in its walls, e.g. *Elytrophalloides*, and probably serve to transport eggs and spermatozoa along its length by peristalsis. In some genera, such as *Paradinurus* and *Hemiurus*, the proximal part of the hermaphroditic duct is lined by villous, glandular cells of unknown function: this region may serve a similar function to the prostatic vesicle (q.v.) of the lecithochiriines. The distal part of the hermaphroditic duct in *Hemiurus* is lined with cuticular papillate structures: as this is the region which forms the outer surface of the temporary sinus-organ, it presumably aids the maintenance of the union during copulation. There are indications in *Halipegus* that the hermaphroditic duct in some species of this genus may be transitory, developing from the sinus-organ as it extends.

The absence of an hermaphroditic duct, except in the case of the Hirudinellidae and in *Halipegus*, is of generic importance only, because of: (1) the inability to distinguish it in some cases from the genital atrium; and (2) the fact that degeneration of the terminal genitalia, due to the increasing importance of self-insemination, appears to have occurred independently on a number of occasions.

Hermaphroditic sac – see *sinus sac*.

Inner vesicle – this is the name given by Juel (1889) to the sac-like structure (Fig. 3), filled with active and/or disintegrating spermatozoa found within the structure which we have called Juel's organ (q.v.). In the rudimentary form of Juel's organ (see *rudimentary Juel's organ*) this sac-like structure has not been enveloped, and is referred to here as a 'rudimentary seminal receptacle' (q.v.). According to Juel (1889) and Lander (1904), the inner vesicle normally appears to have an aperture at its distal end, and presumably it is through this that the disintegrating spermatozoa and vitelline material pass into the outer, amorphous mass of Juel's organ. The inner vesicle, which may be oval or in the form of a convoluted tube, appears to act, therefore, as a 'killing chamber' for the excess reproductive material.

This structure is present in all of the groups where a fully developed Juel's organ occurs, and its taxonomic significance is as discussed for the latter organ. It should be noted that in the case of certain didymozooids the inner vesicle does not appear to be entirely enveloped by the outer mass of Juel's organ.

Juel's organ – in many hemiuroids, and all hemiurids, Laurer's canal does not open dorsally, but leads into an organ which has been referred to as a 'seminal receptacle' or, more recently 'the pouch of Laurer's canal' (Madhavi & Rao, 1974). It was apparently first described by Juel (1889), and we, therefore, felt (Gibson & Bray, 1975) that Juel's organ was an appropriate designation. It consists of an oval or globular sac containing an amorphous granular material, with the occasional (?) amoeboid cells embedded in it (Figs 3A & 4A). An 'inner vesicle' (q.v.), either globular and/or tubular, lies within this mass and contains spent (but often active) or partly disintegrated spermatozoa, vitelline material and, occasionally, ova. The inner vesicle is fed by Laurer's canal, which may be long or short, depending upon the proximity of Juel's organ to Mehlis' gland. The other end of the inner vesicle opens into the outer mass of Juel's organ. Sometimes Juel's organ and Mehlis' gland are apparently enclosed by a common membranous sheath, but in other species Juel's organ lies outside the sheath surrounding Mehlis' gland.

The function of Juel's organ is, apparently, as a disposal unit for excess reproductive material, which enables these resources to be recycled and is thus economically advantageous to the worm compared with the situation where Laurer's canal acts as a drain for these products. It is possible
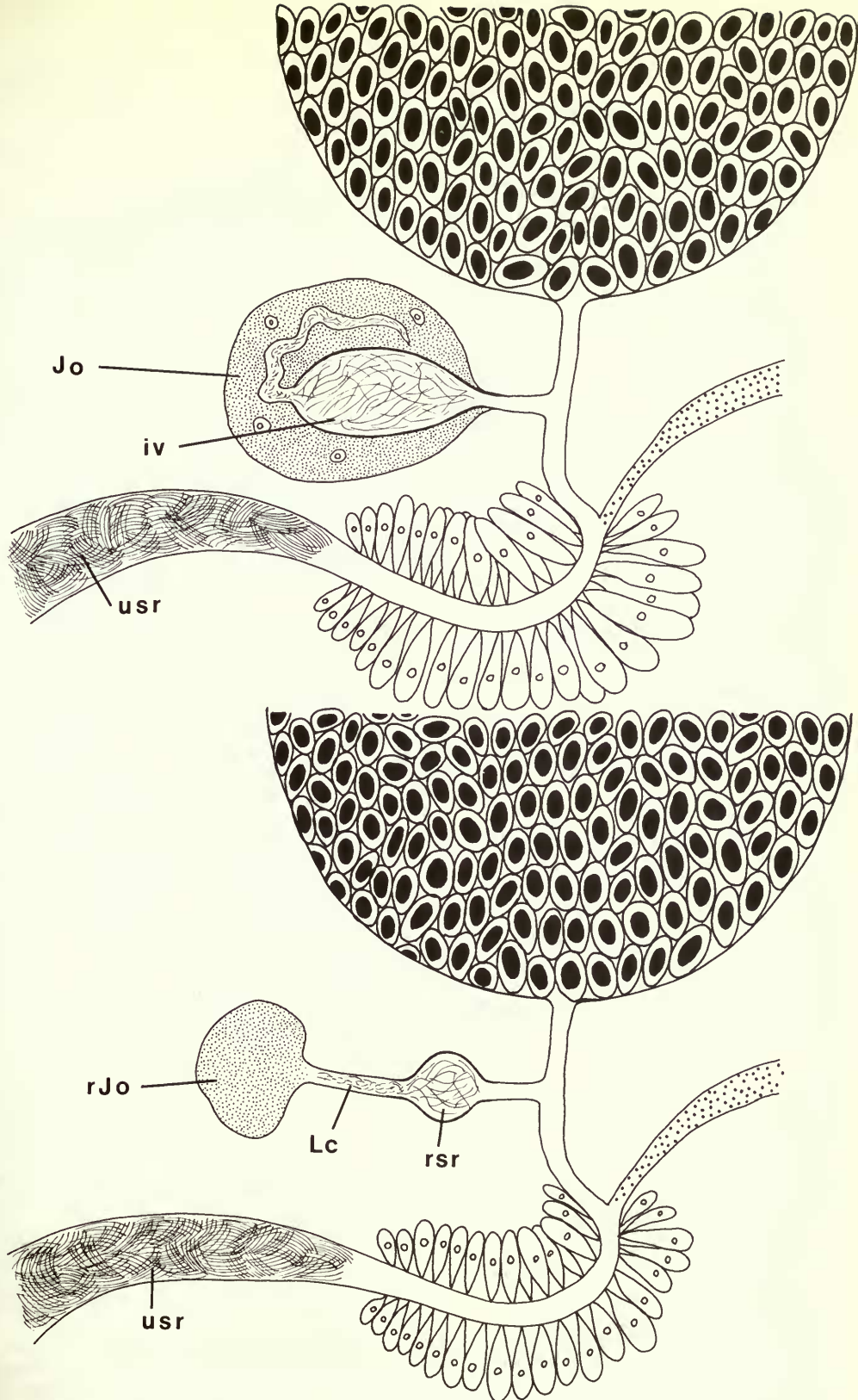
Fig. 3 Diagrammatic representation of a fully developed (A) and a rudimentary (B) Juel's organ. [iv, 'inner vesicle'; Jo, Juel's organ; Lc, Laurer's canal; rJo, rudimentary Juel's organ; rsr, rudimentary seminal receptacle; usr, uterine seminal receptacle.]

that the (?) amoeboid cells in the outer mass of Juel's organ might be involved in the final break-down of this waste material. A fully developed Juel's organ is found in all hemiurids (*sensu stricto*), the aphanurine bunocotylids, the dictysarcids, the hysterolecithine lecithasterids and in some halipegine derogenid genera. It also occurs, in a slightly modified form, in the nemato-bothriine didymozooids.

In certain derogenine and sclerodistomid genera Juel's organ possesses no inner vesicle. This form, which we consider to be more primitive, we have referred to as a 'rudimentary Juel's organ' (q.v.). In this case there is usually a rudimentary seminal receptacle (q.v.), from which the 'inner vesicle' is later formed, that leads via a region of Laurer's canal of varying length into an amorphous mass, resembling the outer region of the fully developed Juel's organ (Figs 3B & 4B). The presence of a fully developed Juel's organ we consider to be a feature of significance at the subfamily level, except in the case of the Halipeginae, where it is of generic importance only (but see *Genarchopsis*).

Laurer's canal – a duct which links the oviduct with either the exterior, a seminal receptacle (q.v.) or with Juel's organ (q.v.). Its function has long been a matter of contention. Looss (1893) wrote a paper entitled, 'Ist der Laurers'che Kanal der Trematoden eine Vagina?' and he, Goto (1893) and Johnston (1912) believed that it functioned as a 'sperm-drain'. Cohn (1902, 1903) and Palombi (1931), however, have described examples where Laurer's canal is used as a vagina. This work led Hyman (1951) to state, 'Laurer's canal in flukes was formerly considered to serve as an exit for superfluous sperm and yolk cells but is now known to function in copulation'. Our recent work (Gibson & Bray, 1975) with hemiuroids has indicated that Laurer's canal does in fact function in this group as a drain for excess and/or spent seminal and vitelline material, and we suggest that in other groups the use of this canal as a vagina during copulation is a more recent development associated with the loss of a uterine seminal receptacle (q.v.) and the development of a functional seminal receptacle as a proximal dilation of this canal, i.e. a canalicular seminal receptacle (q.v.). It should be noted that Juel's organ appears to be a modification of Laurer's canal. The nature of Laurer's canal and its presence or absence are often useful features at the subfamily or family level, except in the cases of the Derogeninae, Halipeginae, Prosorchiinae and Trifoliovariinae.

Manter's organ (*accessory excretory organ* or *vesicle*) – a tubular vesicle lined with an epithelium and usually surrounded by bundles of muscle, especially longitudinal muscle. It occurs dorsal to the excretory vesicle (q.v.) into which it opens postero-ventrally close to the excretory pore. It is a feature of the Scerodistomidae, occurring singly in *Prosogonotrema*, *Prosorchis* and *Prosorchiopsis* and paired in *Sclerodistomum*. Gibson & Bray (1977) suggest that it might occur in *Distoma gigas* Nardo, 1827, a giant digenean of uncertain systematic position. The name Manter's organ appears to have been coined by Yamaguti (1971), and is in our opinion more acceptable than the appellation 'accessory excretory organ (vesicle)', as the function of this organ is unknown.

Mehlis' gland – a cluster of gland-cells which surround the region of the ovovitelline canal which links the oviduct and the uterus: this is usually the region of the oötype (q.v.). It is thought to produce a mucous secretion which lubricates the uterus and a lipoprotein secretion which forms a membrane around the ovum and vitelline cells upon which shell-material is then deposited (Smyth, 1966). It also seems likely that it may produce a secretion which activates the spermatozoa.

Mehlis' gland appears to be of little systematic importance, except that, although in the majority of hemiuroids it is post-ovarian [the oviduct leaves the ovary posteriorly], in the azygiids and accacoeliine accacoeliids it is pre-ovarian [the oviduct leaves the ovary anteriorly]. It is likely that there are several exceptions to this rule, such as the prosorchiine sclerodistomids. In certain hemiuroids Mehlis' gland appears to be enclosed along with Juel's organ by a membranous sac (see Madhavi & Rao, 1974).

Metraterm – a name given to the terminal region of the uterus, when it can be distinguished morphologically from the rest of this organ. It is of little taxonomic importance in this group, as it is usually difficult to distinguish and often tends to grade into the uterus-proper. It is usually
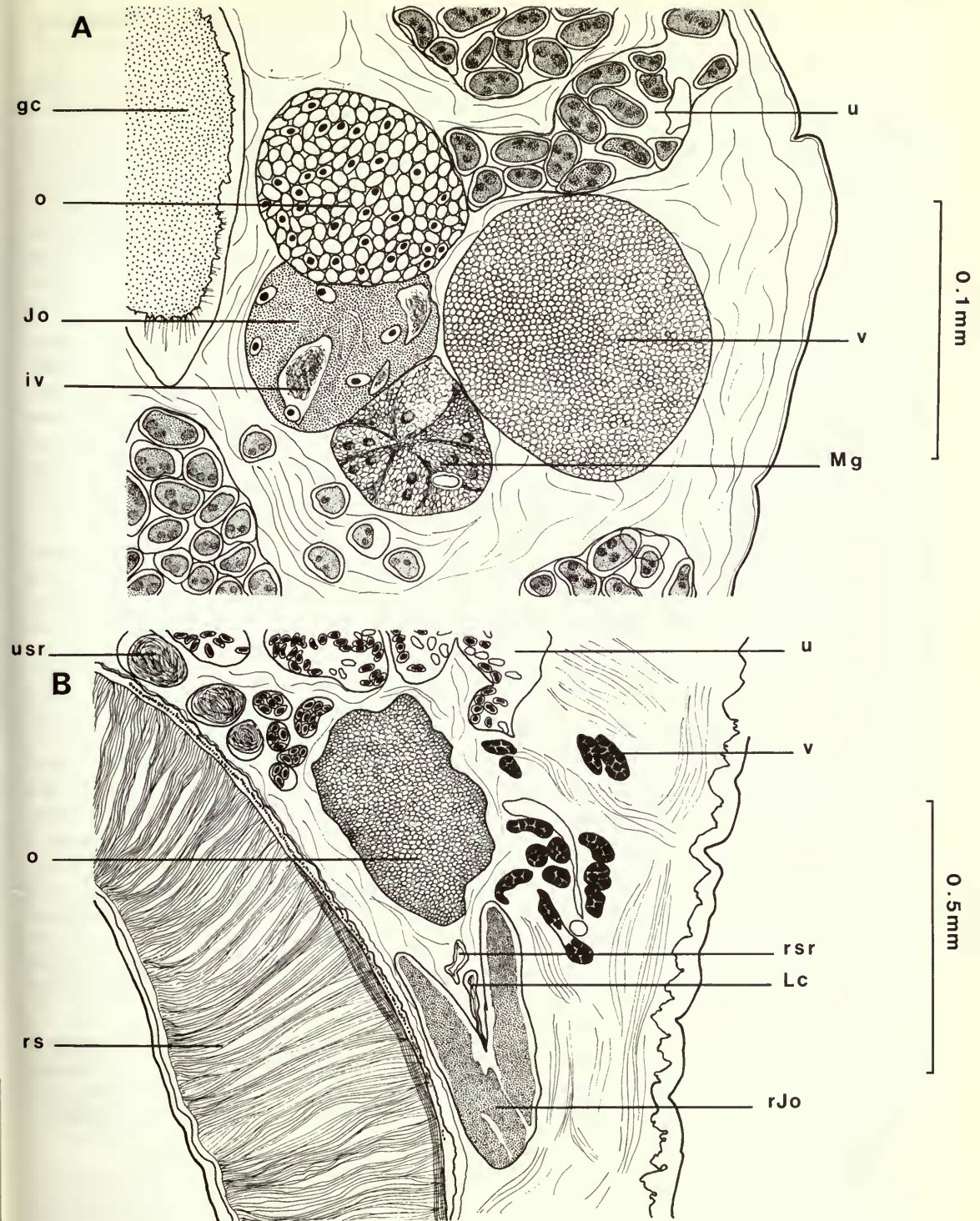
Fig. 4 Sections of a fully developed (A) and a rudimentary (B) Juel's organ. [gc, gut-caeca; iv, inner vesicle; Jo, Juel's organ; Lc, Laurer's canal; Mg, Mehlis' gland; o, ovary; rJo, rudimentary Juel's organ; rs, ventral sucker; rsr, rudimentary seminal receptacle; u, uterus; usr, uterine seminal receptacle; v, vitellarium].

muscular, often surrounded by small gland-cells and in some dinurines it has a villous lining. In *Erilepturus* (= *Uterovesiculurus*) it appears to form a distinct dilate sac.

Oötype – a region of the female duct (ovovitelline canal) where egg-formation and possibly fertilization occur. This is normally the region, surrounded by Mehlis' gland (q.v.), which links the oviduct with the uterus. In the hemiuroids this region does not appear to be vesicular as in many other digeneans, but is present as a narrow tube. Although we have seen soft egg-shells in this region in *Isoparorchis*, *Otodistomum* and some hemiurids, in others, such as *Derogenes*, *Pulmovermis* and *Syncoelium*, the oötype appears to extend into the first part of the uterus, as egg-shell formation occurs in a region not surrounded by Mehlis' gland. We are referring to this region as a *uterine oötype* (q.v.). The systematic significance of these variations of the oötype have not been studied; but it seems unlikely that they may be of any value above, perhaps, the generic level.

Ovary – in the hemiuroids this is usually oval in shape, but in certain groups, such as the lecithasterids, syncoeliids and dictysarcids, it is commonly composed of 4 or 5 distinct lobes. In one instance (*Isoparorchis*) the ovary is tubular. The position of the ovary in relation to the testes is an important systematic criterion at the subfamily level, except in the case of some of the macrodeninine lecithasterids. The ovary is post-testicular in most groups, but is pre-testicular in the azygiine azygiids, the ptychogonimids, the gonocercine derogenids and certain macradeninine lecithasterid genera, and occurs between the testes in the bathycotylids. The ovary occurs in the hindbody in all groups, except for the prosogonotrematine sclerodistomids.

Oviduct – the duct linking the ovary and the oötype (q.v.). It receives Laurer's canal and the common vitelline duct before, or sometimes in the case of the common vitelline duct, slightly after entering Mehlis' gland (q.v.). The oviduct appears to leave the ovary posteriorly in the majority of hemiuroids, the exceptions being the azygiids, the accacoeliine accacoeliids and possibly odd genera, such as *Prosorchiopsis*, in other groups.

Pars prostatica – the region of the male duct between the seminal vesicle and either the ejaculatory duct or the hermaphroditic duct. It is normally surrounded by prostatic gland-cells and lined by what appear to be anuclear gland-cells which often project into the lumen presenting a papillate or villous appearance: it is possible, however, that the latter are merely internal extensions of the outer gland-cells. The function of this region is not known for certain, but it may produce a secretion which protects and lubricates the spermatozoa during ejaculation. It may also be involved in the activation of spermatozoa during ejaculation. The shape of this duct, i.e. whether it is vesicular or tubular, is of specific value, and so is its length. The presence of a vesicular pars prostatica has often been confused with a prostatic vesicle (q.v.). When the external gland-cells are severely restricted in their distribution by surrounding parenchyma or are bound by a fibrous membrane, they are spoken of as being 'delimited'. In certain cases an aglandular duct links the pars prostatica and the seminal vesicle; this is usually referred to as a tubular extension of the seminal vesicle or as an aglandular region of the pars prostatica. An aglandular region also links the two parts of the pars prostatica in the dinurine hemiurid *Mecoderus*.

Peduncle – this is a stalk upon which the ventral sucker may be surmounted. It occurs only in a few species of hemiuroids. It may be of some taxonomic importance at the generic level; but it is often variable in size, sometimes being either difficult to distinguish or prominent in the same species, e.g. in *Accacladium serpentulum* Odhner, 1928, as described by Bray & Gibson (1977).

Permanent sinus-organ – see *sinus-organ* (*permanent*).

Plications – regular backwardly directed thickenings of the tegument which surround or partly surround the body transversely. They are a feature unique to the hemiurids and the aphanurine bunocotylids; but only occur in certain genera, being a feature normally considered to be of systematic importance at the generic level (a notable exception being the genus *Aphanurus*, but see p. 65). They may occur over the whole body (soma) or just part of it, and tend to be better developed anteriorly than posteriorly, especially in the dorsal field. They are never present on the

ecsoma. Care should be taken not to confuse these regular tegumental thickenings with a rugate appearance caused by contraction, with small transverse ridges caused by circular muscles in the body-wall of poorly preserved material (these do occur on the ecsoma), and with transverse folds of the body-wall surrounding the suckers of certain bunocotylid genera.

Plications appear to be a primitive hemiurid feature which arose in association with the ecsoma (q.v.). They are possibly a feature which permits the thickening of the somatic tegument during periods of low pH or high osmolarity when the ecsoma is withdrawn, and yet still allows full and easy extension and contraction of the body during periods of activity. Certain genera, which possibly no longer inhabit the pyloric region of the stomach or which are parasitic in physiologically 'stomachless' fish (see Barrington, 1957), have lost this feature.

Pre-acetabular pit – see *presomatic pit*.

Precaecal sac – see '*Drüsenmagen*'.

Pre-oral lobe – a small region of the body anterior to the oral sucker. In some instances it may actually overhang the anterior margin of the oral sucker. It has no apparent systematic importance, except that it is glandular in one species of *Otodistomum* (see Gibson & Bray, 1977), as it appears to occur, at least to some extent, in all hemiuroids.

Presomatic pit (*preacetabular pit*) – a deep, concave depression, circular or oval in section, which is present mid-ventrally just anterior to the ventral sucker. It occurs in certain lecithochiriine genera, in the plerurine genus *Synaptobothrium* and apparently in the aphanurine genus *Mitrostoma*. Great care should be taken in its use as a taxonomic criterion as it is easily confused with the ventro-cervical groove (q.v.), which is common in many hemiurids. In the genus *Lecithochirium* this structure can be either present or absent, being very small and difficult to distinguish in the type-species: this does not appear, therefore, to be a useful character in distinguishing *Lecithochirium* and *Sterrhurus* (see p. 93).

The presomatic pit often has a region of glandular tissue around its base; but its actual function is not understood. Lloyd (1938) has suggested that it acts as a chemo-sensory organ and that it may be associated with the extrusion and withdrawal of the ecsoma: it would appear that the latter certainly cannot be the case in *Mitrostoma*.

Prostatic sac – a term coined by Gibson (1976) for the muscular sac which surrounds the pars prostatica and the seminal vesicle of the azygiids. Its function is not known for certain, but presumably it aids the evacuation of spermatozoa and prostatic secretion during ejaculation.

Prostatic vesicle – a dilation of the ejaculatory duct within the sinus-sac, which is usually lined by glandular cells and occurs in addition to an external pars prostatica. Essentially, it is identical to an ejaculatory vesicle (q.v.), except for the presence of the glandular cells. As the latter cells can apparently be lost, it does seem unwise to distinguish a prostatic vesicle from an ejaculatory vesicle, and, in view of the possibility of confusing the former structure, both nomenclaturally and morphologically, with a 'vesicular pars prostatica' (q.v.), it might be advisable to refer to the prostatic vesicle as being a 'glandular ejaculatory vesicle'. This structure occurs for certain only in the lecithochiriine, glomericirrine and hypohepaticoline genera, and is possibly a feature of importance at the subfamily level (if included as a type of ejaculatory vesicle). We do not consider that this structure occurs in any of the plerurine or pulmovermine genera, for in these cases the pars prostatica itself appears to be partly enclosed by the sinus-sac in cases when the latter is present. The function of a prostatic vesicle is probably identical to that suggested for an ejaculatory vesicle.

Receptaculum seminis – see *seminal receptacle*.

Receptaculum seminis uterinum – see *uterine seminal receptacle*.

Rudimentary Juel's organ – a form of Juel's organ (q.v.) which lacks an 'inner vesicle' (q.v.). It has a granular appearance and is present usually at the distal end (Figs 3B & 4B), but occasionally more proximally, of Laurer's canal. It presumably has a similar function to a fully developed Juel's organ, into which it has probably evolved in more advanced forms by enveloping the

rudimentary seminal receptacle (q.v.) and forming an 'inner vesicle'. Small, black structures can be seen within the amorphous mass which fills this organ: we wonder whether these might be bacteria which may carry out the final breakdown of the excess seminal and vitelline material, much as we suggest that (?) amoeboid cells might do in a fully developed Juel's organ.

A rudimentary Juel's organ is known to occur in certain derogenine derogenid and prosogonotrematine and prosorchiine sclerodistomid genera, but its taxonomic significance, even at the generic level, is uncertain. This organ also appears to occur in the aspidogastrean *Aspidogaster conchicola* von Baer, 1826 (see p. 123).

Scales – a term used by Manter (1934) to describe the structures on the tegument of *Dinosoma*. We believe that they are probably just regularly crenulate plications (q.v.).

Seminal receptacle – a general term covering several different types of apparatus for the storage of spermatozoa in the female reproductive system. In our opinion the various forms of seminal receptacle should be clearly differentiated in descriptions, as they are important taxonomic criteria. We recognize four different kinds of seminal receptacle present in the Hemiuroidea (Fig. 1): (1) a 'blind seminal receptacle' (q.v.), which is a blind sac, linked to the oviduct by a short tube, occurring in most of the lecithasterid subfamilies, the opisthadenine bunocotylids and the derogenid genus *Leurodera*, and which appears to have evolved from Juel's organ (q.v.) or in some cases from a rudimentary or canalicular seminal receptacle; (2) a 'canalicular seminal receptacle' (q.v.), which is a large proximal dilation of Laurer's canal, and occurs frequently in other groups of digeneans, but apparently within the Hemiuroidea it occurs for certain only in the lecithasterid genus *Trifoliovarium* and in a modified form in the derogenid genus *Progonus*; (3) a 'rudimentary seminal receptacle' (q.v.), which is a small proximal dilation of Laurer's canal that, when present, always occurs together with a uterine seminal receptacle, but this form differs from the others in that it is not a store of fresh, quiescent spermatozoa and in that the small amount of spermatozoa which it does contain are spent, although often still active; and (4) a 'uterine seminal receptacle' (q.v.), which is a store of spermatozoa present in the proximal region of the uterus, and occurs in the majority of hemiuroids. Another type is an 'oviducal seminal receptacle', which is formed as a dilation of the oviduct; but this type does not occur in the Hemiuroidea. With the exception the 'rudimentary' and 'uterine' types, the various forms of seminal receptacle do not normally occur together in the same individual.

Seminal sac – a term used by Manter (1947) for an oval, muscular sac which encloses a convoluted, tubular seminal vesicle in the bunocotylid *Opisthadena dimidia* Linton, 1910. It appears to be a modification of the muscular type of seminal vesicle where the muscular wall is clearly not associated with the membranous lining of the seminal vesicle. It also occurs in some of the other species of *Opisthadena* and in the hemiurid *Elytrophalloides*.

Seminal vesicle – a dilation of the vas deferens (q.v.) which forms a store of spermatozoa which is ready for ejaculation. It is often provided with a muscular wall or with sphincter muscles which constrict it into portions. These modifications, which are often of systematic importance at the generic level, are involved with the evacuation of spermatozoa from the seminal vesicle, through the pars prostatica and into the hermaphroditic duct, often against the hydrostatic pressure produced by the sinus-sac (q.v.). The shape of the seminal vesicle is also often of specific or generic value, as is its position in relation to the ventral sucker. In the more primitive forms it is usually tubular. In the hemiuroids the seminal vesicle is normally free in the parenchyma, but in certain halipegine derogenids it may be partly or completely enclosed within the sinus-sac, in the azygiids it is contained within a prostatic sac (q.v.), and in certain species of *Opisthadena* it forms a 'seminal sac' (q.v.).

Sinus-organ (*permanent*) – a copulatory organ of variable size which is usually formed externally from the wall of the normally well-developed genital atrium and internally from the hermaphroditic duct. This type of sinus-organ is contractile, but is still visible in sections as a small cone when completely retracted. It usually occurs in one of two forms, although intermediate forms are sometimes found (Fig. 5):
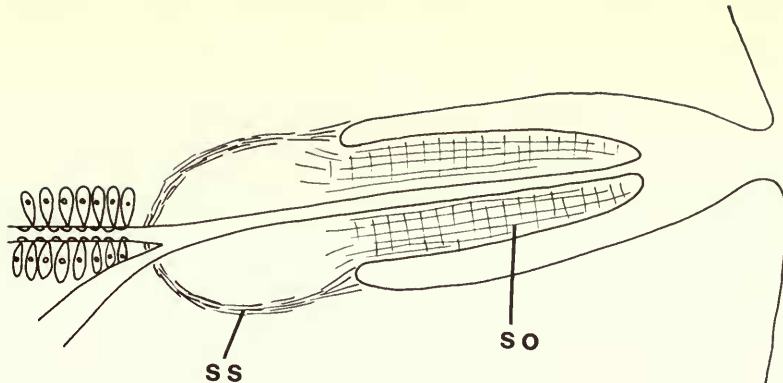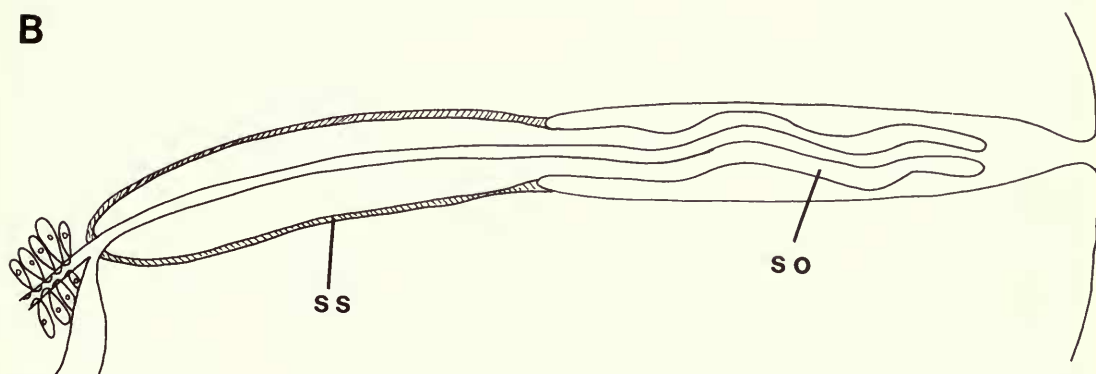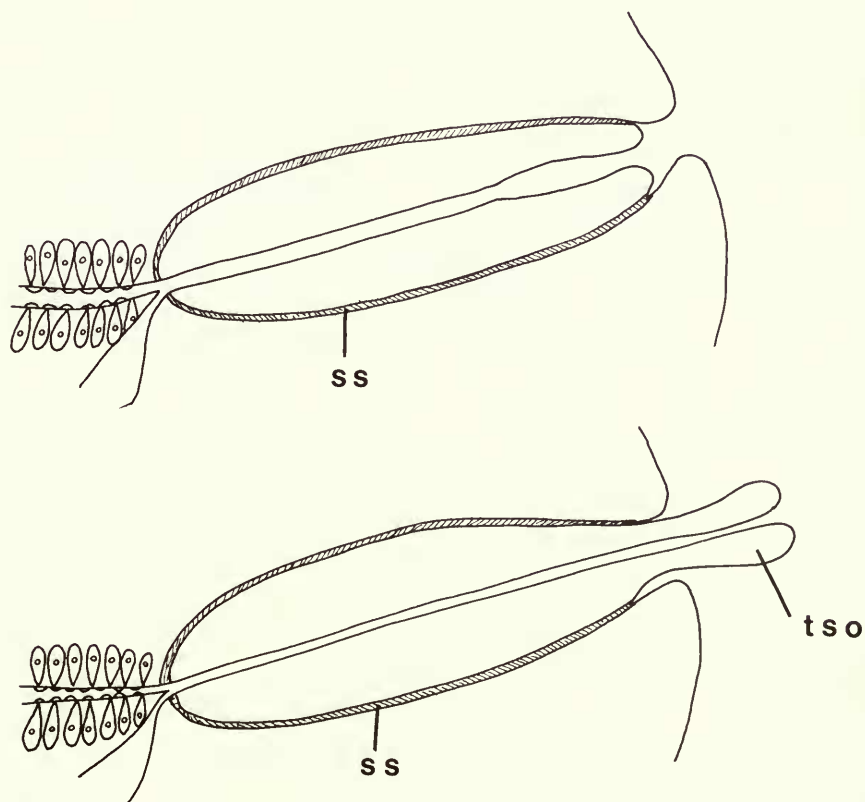
Fig. 5 The types of sinus-organ occurring in the Hemiuroidea: A. Muscular sinus-organ; B. Amuscular sinus-organ; C. Temporary sinus-organ. [so, permanent sinus-organ; ss, sinus-sac; tso, temporary sinus-organ.]

(1) 'Muscular' – where it is probably everted entirely or partly by its own intrinsic musculature (when partly, the remaining force is supplied by hydrostatic pressure produced by the sinus-sac: see Gibson & Bray, 1974): this form occurs in many of the more primitive hemiuroid groups (see p. 129);

(2) 'Amuscular'* – a form, associated with the presence of a thick-walled (muscular) seminal vesicle, which is probably everted entirely, or almost entirely, by hydrostatic pressure produced by the sinus-sac upon its contents: this form occurs in the elytrophalline and glomericirrine hemiurids, the muscular seminal vesicle being required to force spermatozoa into the hermaphroditic duct against the hydrostatic pressure built up by the walls of the sinus-sac.

The presence or absence and type of sinus-organ are often useful taxonomic criteria up to the subfamily level; but the sectioning of specimens is essential and great caution must be exercised in the use of this feature. See *sinus-organ (temporary)*.

Sinus-organ (temporary) – an amuscular or weakly muscled copulatory organ, formed from the hermaphroditic duct by hydrostatic pressure within the sinus-sac, which is a transitory structure (Fig. 5). It is usually only present during copulation, but also occurs occasionally in fixed specimens. The genital atrium is usually small or apparently absent in forms with a temporary sinus-organ. Naturally 'permanent' [see *sinus-organ (permanent)*] and 'temporary' types of sinus-organ cannot occur in the same species of worm. The two forms, however, may be difficult to distinguish when only a small number of specimens is available for study. A temporary sinus-organ may be associated with slight thickenings in the wall of the seminal vesicle, but is more often associated with the presence of sphincter muscles which tend to partition the seminal vesicle and are capable of exerting pressure, thus forcing spermatozoa into the sinus-sac against its internal hydrostatic pressure during ejaculation. As the genital atrium tends to be short or absent, the temporary sinus-organ itself is also short, and, therefore, the hydrostatic pressure required to extrude it is reduced. The sinus-sac tends, therefore, to be smaller than in forms with an amuscular permanent sinus-organ. A temporary sinus-organ occurs in the more advanced forms of hemiurids, bunocotylids and lecithasterids. As this transitory structure is rarely seen everted, it is of no systematic significance.

Sinus-sac or hermaphroditic sac – a muscular sac which surrounds the base of the genital atrium, if present, and encloses the hermaphroditic duct and/or the terminal portions of the ejaculatory duct and uterus. Its apparent function is to aid the eversion of a permanent sinus-organ (q.v.) or the production of a temporary sinus-organ (q.v.) from the hermaphroditic duct. It may also aid the expulsion of spermatozoa and eggs, especially the former in cases where an ejaculatory (or prostatic) vesicle (q.v.) or the seminal vesicle is enclosed within the sinus-sac. In certain instances, e.g. in some of the plerurine hemiurids, there may be a large proximal gap in the wall of the sinus-sac at the point through which the male and female ducts pass: this is known as an 'open-type' of sinus-sac and is probably a vestigial form. In other groups of hemiuroids the sinus-sac may be reduced, or in some cases completely lost. Sectioning is essential when the sinus-sac is apparently absent, as the vestiges of this structure are often insignificant. This feature is frequently of some importance at the family level, as it is missing in the Azygiidae and Hirudinellidae, which possess a 'prostatic sac' (q.v.) and a 'cirrus-sac' (q.v.), respectively; but great care should be exercised in the utilization of this feature, as it appears to have been lost independently in certain genera from a number of distantly related hemiuroid groups, e.g. *Gonocerca*, *Syncoelium*, *Tetrochetus*, *Prolecitha* and *Bunocotyle*.

Temporary sinus-organ – see *sinus-organ (temporary)*.

Testes – there are usually two globular testes present in hemiuroids. Exceptions are the syncoeliids, which either have a much larger number (11–18) of large oval masses (referred to as testes, although there are only two vasa efferentia) or possess apparently follicular testes, and two lecithasterid genera, *Monorchiaponurus* and *Monorchimacradena*, which are reported to have one testis.

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* Presumably there are some longitudinal muscle fibres present which permit contraction of this type of sinus-organ.

An important feature at the subfamily level (except in some members of the Macradeninnae) is the relationship between the ovary and the testes, the ovary usually being post-testicular. In the azygiine azygiids, the ptychogonimids, the gonocercine derogenids and certain macradeninine lecithasterids, however, it is pretesticular, and in the bathycotylids it is inter-testicular. The relative positions of the testes and their shape are of little value above the specific level, except that in the dictysarcid genus *Elongoparorchis* they do appear to be consistently elongate. The testes normally occur in the hindbody, except in the prosogonotrematine and prosorchiine sclerodistomids.

Uroproct – the aperture of the excretory vesicle when the base of the latter organ communicates directly with the distal extremities of the gut-caeca. A uroproct, therefore, serves as an orifice for the evacuation of waste-products from both the excretory and alimentary systems. This structure occurs independently and regularly in the Accacoeliidae, Hirudinellidae, Ptychogonimidae and Otiotrematinae, but, except for the Accacoeliinae and the Ptychogonimidae, it does not occur in all of the genera in these groups. It is normally considered to be a feature of generic importance.

Uterine oötype – the proximal region of the uterus, present in some species, into which the region of egg-formation extends. Its systematic importance is not understood. See *oötype*.

Uterine seminal receptacle or *receptaculum seminis uterinum* – a term given to the proximal region of the uterus when it is filled with 'fresh' spermatozoa and is, therefore, acting as a seminal store (Fig. 1). This region can normally only be differentiated from the remainder of the uterus by the presence of spermatozoa. It is the commonest form of seminal receptacle (q.v.) present in the Hemiuroidea, being absent only in the lecithasterids (with the exception of the Hysterolecithinae), the opisthadenine bunocotylids and in the derogenids *Progonus* and *Leurodera*. This type of seminal receptacle is probably associated with cross-insemination, using the genital atrium as a vagina, or with self-insemination, and differs from all other types of seminal receptacle in that spermatozoa pass towards the ovary through the oötype. In the past many workers have mistaken this structure for a canalicular seminal receptacle (q.v.), but in sectioned material the two can easily be distinguished. Except in the cases of the derogenids *Progonus* and *Leurodera*, the presence or absence of this type of seminal receptacle is an important systematic feature at the subfamily level. Great care must be exercised with the use of this feature because it is by nature transitory, and, when empty, it is not recognizable as a seminal store. We have observed, in sectioned material, specimens of *Hirudinella* and *Prosorchiopsis* (forms possessing a uterine seminal receptacle) which do not have any spermatozoa in the proximal region of the uterus.

Uterus – a duct, normally full of eggs, which links the oötype with the hermaphroditic duct, genital atrium or genital pore. The distal extremity may be modified to a form metraterm (q.v.), and the proximal extremity may form a uterine seminal receptacle (q.v.) or a uterine oötype (q.v.). In addition to transporting eggs, the proximal region of the uterus appears to be involved in the hardening and tanning of the egg-shells. The uterus often coils between the ovary and the ventral sucker, but it may loop well posterior to the ovary and in some cases coils in the forebody. Its distribution tends to be of generic importance and occasionally of subfamilial importance, especially in cases where it reaches into the post-ovarian field or is entirely pre-ovarian.

Vasa efferentia – single narrow ducts which connect each testis with the vas deferens (q.v.). In the Syncoeliinae, where there are 11–18 so-called testes, there are the usual two vasa efferentia, and the ducts linking these testes to the vasa efferentia are called 'collecting ducts'. The vasa efferentia are of no apparent systematic importance in the Hemiuroidea.

Vas deferens – a duct formed by the fusion of the two vasa efferentia (q.v.), which, in almost all cases, is dilate, filled with spermatozoa and referred to as the seminal vesicle (q.v.). In itself, therefore, it is of no systematic importance, although in certain groups there is a narrow duct linking the seminal vesicle with the pars prostatica (q.v.).

Ventro-cervical groove – a transverse crevice which occurs on the ventral surface immediately anterior to the ventral sucker in many hemiurids. It appears to have no actual function, as it is

simply caused by the close proximity of the oral and ventral suckers in some of these genera. The size of this feature appears to be dependent upon the degree of contraction which occurs in the forebody during fixation. It appears to have no systematic value, except that it has occasionally been mistaken for a presomatic pit (q.v.).

Vitellarium – a structure of variable morphology that produces vitelline (yolk) cells which accompany the ovum in egg-formation. The form of the vitellarium is a valuable taxonomic criterion ranging from the species to the family level. The common arrangements of the vitellarium in the Hemiuroidea are as follows (see Fig. 7): (1) follicular; (2) linked follicles, giving a chain-like tubular arrangement; (3) convoluted tubules which are often branched; (4) about seven tubules, usually arranged four on one side of the body and three on the other; (5) about seven oval to digitiform lobes; (6) two oval or slightly lobed masses; and (7) a single oval mass. These forms tend to grade into one another, but it is noticeable that the seven-lobed vitellarium occurs widely throughout the group. The arrangement of the vitellarium is discussed in more detail on p. 124. One unusual feature occurs in the Accacoeliinae, where the sinistral side of the system is reduced to a vestige. In certain instances, especially in the Lecithasteridae and the Derogenidae, the relationship between the vitellarium and the ovary is useful systematically; but the vitellarium or at least the origin of the main vitelline ducts is usually post-ovarian, although exceptions to this include the azygiids and the accacoeliine accacoeliids.

III. A classification of the Hemiuroidea with keys and definitions

Introduction

The following classification, which we propose for the Hemiuroidea, is based upon adult morphology associated with an attempt to understand the function of the organs and organ-systems (see p. 39). This relies heavily upon comparative morphology, as do most of the previous classifications. The main problem with this, as discussed above, is that much of the descriptive work over the years has been inadequate. Many workers around the turn of the century gave detailed and careful descriptions, based upon sectioned material. Work of this standard has been the exception, rather than the rule, since that time. In attempting to provide a feasible classification we have, therefore, examined as many species as possible, both in serial sections and whole-mounts. The lack of certain material has left large gaps, which have had to be filled with a critical appraisal of the literature. In certain groups, and in particular in many individual genera, much of the detail necessary to classify the animals has not been supplied by the original authors. In these cases our classification is particularly tentative, and we have usually indicated where we consider our knowledge to be totally inadequate. In some instances, using our knowledge of the groups as a whole and assessing the functional requirements present, we have assumed the morphology of certain undescribed or apparently wrongly interpreted structures. While this may seem somewhat unsatisfactory, some of our interpretations were proved correct during the course of the work, e.g. before specimens were obtained we correctly assumed the presence of a sinus-sac, rather than a cirrus-sac, in *Arnola* and *Glomericirrus*, and we correctly assumed the presence of Juel's organ in *Elongoparorchis* and in many of the hemiurids (*sensu stricto*).

As far as the systematics of this group is concerned, we have faced many problems in weighing the relative values of different factors. At one time we were inclined to give considerable weight to the details of the terminal genitalia, and also to the vitellarium. While these factors may have significance at the generic or subfamily level, they do seem to be susceptible to development or regression in certain groups. The details of the proximal region of the female system have, we believe, a fundamental value in distinguishing subfamilies, although there are exceptions to this, for in the Derogenidae and the Trifoliovariinae a variety of conditions occur. The presence of Juel's organ, for example, seems to be of considerable importance; but, even in this case, care has to be taken, and the complete morphological pattern must be taken into consideration.

Definitions of the taxa are presented; but features common to a group of taxa are given in the definition of the higher taxa, rather than repeated throughout the group. Features, especially

those taken from the literature, which we believe to be questionable, are indicated by question-marks.

Wherever possible material was examined, especially in serial section. The abbreviations used to indicate what material we have seen are given after the generic name, and are as follows: T=type-material of type-species; t=non-type material of type-species; n=material of non-type-species; w=whole-mount; s=serial sections. The absence of this information indicates that the data have been derived from the literature.

We have attempted to provide dichotomous keys to the taxa. Rather than relying upon the most obvious of criteria, we have tried to produce keys which work, with the result that the sectioning of material, while always advisable, may in fact be essential. These keys must be used with care, and with the understanding that this classification is based upon polythetic assemblages of characters. Soft-bodied animals, such as digeneans, give few good metrical or meristic characters, so that it is very important to possess a good understanding of the overall morphology while attempting to determine these worms.

Some readers may note that the authorities which we have given for some of the family-group names differ from those presented by some other workers. These workers appear to have followed a recent trend which tends to confuse systematics and nomenclature. In using the authority for the original mention of the family-group name, irrespective of suffix, we are following Article 36 of the International Code of Zoological Nomenclature.

As with any work of this kind, our classification must be considered provisional. We hope that it may be helpful in stimulating and encouraging a closer and more careful examination of the worms in this group.

Superfamily **HEMIUROIDEA** Looss, 1899

Azygioidea Lühe, 1909
Accacoelioidea Odhner, 1911
Isoparorchioidea Travassos, 1922

Body small to large; oval to cylindrical. Ecsoma present or absent. Body-surface smooth, rugate or plicated (or 'scaley'); never spiny, but occasionally papillate. Oral and ventral suckers well developed, occasionally small. Ventral sucker normally in middle or anterior half of body, occasionally just inside posterior half of body; occasionally pedunculate. Prepharynx absent. Pharynx well developed; normally oval, occasionally modified. Oesophagus usually short, occasionally long. 'Drüsenmagen' present or absent. Gut-caeca usually end blindly near posterior extremity, occasionally form cyclocoel or uroproct. Testes normally two, rarely one or follicular; normally tandem to symmetrical, preovarian and near middle of body; occasionally in forebody or post-ovarian. Seminal vesicle oval to tubular; occasionally constricted into portions usually thin- but occasionally thick-walled; in fore- or hindbody; normally external to sinus-sac, rarely partly or entirely internal. Pars prostatica tubular to vesicular; long or short; normally external to sinus-sac, rarely internal; usually in forebody, occasionally entirely inside, or extending into, hindbody. Ejaculatory duct usually present; usually short; often within sinus-sac or sinus-organ; normally unites with metraterm to form hermaphroditic duct; occasionally within 'cirrus-sac'. Hermaphroditic duct usually present; usually within sinus-sac and/or sinus-organ. Sinus-sac present or absent; oval to cylindrical; normally enclosing ejaculatory duct and part of metraterm and/or hermaphroditic duct; occasionally additionally enclosing ejaculatory (prostatic) vesicle or seminal vesicle and/or pars prostatica. Permanent sinus-organ present or absent within genital atrium; conical to tubular; muscular or non-muscular. Temporary sinus-organ sometimes formed from hermaphroditic duct. 'Cirrus-sac', enclosing ejaculatory duct only, and 'cirrus' rarely present. Genital atrium large, small or absent. Common genital pore mid-ventral in forebody. Ovary usually oval, occasionally lobed, rarely tubular or follicular; usually post-testicular, occasionally pre-testicular, rarely inter-testicular; normally in hindbody, rarely in forebody. Mehlis' gland usually post-ovarian, occasionally pre-ovarian. Uterine seminal receptacle plus Laurer's canal and/or Juel's organ *or* blind seminal receptacle alone normally present. Uterine coils usually fill much of hindbody, occasionally extending well into forebody, rarely entirely in forebody. Eggs normally oval; usually small, numerous; occasionally with spine, filament(s) or

threads. Vitellarium normally follicular, tubular or composed of a small number (often *seven*) oval to tubular lobes or one to three (usually two) entire or lobed masses; often post-ovarian, occasionally pre-ovarian; sometimes extending throughout hindbody or into forebody, rarely entirely in forebody. Excretory pore terminal; vesicle Y-shaped; arms united in forebody or not. Manter's organ (accessory excretory vesicle) rarely present. Parasitic in gut, especially stomach, primarily of marine teleosts, but commonly occur in freshwater teleosts and elasmobranchs, occasionally in holosteans, amphibians, reptiles and progenetic in invertebrates; occasionally recorded from gills, skin, body-cavity, swim-bladder and other organs.

Key to Hemiuroidea

1. A. Vitellarium composed of numerous widely distributed follicles . . . . . . (2)
   B. Vitellarium otherwise, usually composed of a small number of oval to tubular (occasionally branched) lobes or 1–3 distinct oval, lobed or unlobed masses . . . . (3)
2. A. Prostatic sac present; parasitic in elasmobranchs and freshwater teleosts
                                                        AZYGIIDAE (p. 60)
   B. Prostatic sac absent; parasitic in gut of elasmobranchs . **PTYCHOGONIMIDAE** (p. 110)
3. A. Testes 2, occasionally 1 . . . . (4)
   B. Testes follicular, 11–18 large or many small follicles arranged in rows or irregularly distributed; usually parasitic in buccal or branchial cavities or on skin (? occasionally internally) of elasmobranchs and marine teleosts . . . **SYNCOELIIDAE** (p. 114)
4. A. Ecsoma absent (take care with this observation as some hemiurids have a reduced ecsoma and some bunocotylids may retain the vestige of an ecsoma) . . . . . (5)
   B. Ecsoma present (sometimes very reduced); body surface often plicated; Juel's organ and uterine seminal receptacle present; vitellarium varies between form with 7 tubular lobes and form with 2 distinct oval masses; parasitic mainly in gut of marine teleosts, occasionally present in freshwater teleosts and lung of sea-snakes **HEMIURIDAE** (p. 84)
5. A. Ovary usually post-testicular, occasionally pre-testicular . . . . . . (6)
   B. Ovary inter-testicular; parasitic on gills (? and in stomach) of marine teleosts
                                                        BATHYCOTYLIDAE (p. 62)
6. A. Ovary oval or lobed . . . . (7)
   B. Ovary tubular; parasitic in swim-bladder of freshwater teleosts **ISOPARORCHIIDAE** (p. 100)
7. A. Ventral sucker anterior to middle of body; parasitic in marine teleosts; seminal vesicle never enclosed in sinus-sac . . . . (8)
   B. Ventral sucker usually in or near middle of body, occasionally more anterior; significant proportion of uterus usually present in forebody [a small number of marine forms do possess a ventral sucker in the anterior half of the body and uterine coils which do not extend into the forebody, but these forms also possess a seminal vesicle which is enclosed within the sinus-sac]; vitellarium 1 or 2 masses, entire or lobed (lobes normally shallow, rarely digitate); seminal vesicle in forebody; ovary and vitellarium pre- or post-testicular; parasitic mainly in gut of freshwater and marine teleosts, occasionally in amphibians, reptiles and freshwater shrimps . . . . **DEROGENIDAE** (p. 71)
8. A. 'Cirrus' present, enclosed in 'cirrus-sac'; female duct opens into genital atrium independently; large parasites from gut (? or gills) of marine teleosts (immature forms occasionally present in salmonids) . . . . **HIRUDINELLIDAE** (p. 98)
   B. 'Cirrus' and 'cirrus-sac' absent; male and female ducts normally unite forming hermaphroditic duct, which is often present within a sinus-organ and enclosed by a sinus-sac . (9)
9. A. Parasitic in gut (occasionally on gills) . . . . (10)
   B. Parasitic in swim-bladder or gall-bladder . . . . (13)
10. A. Vitellarium 1, 2 or 3 compact masses . . . . **BUNOCOTYLIDAE** (p. 62)
    B. Vitellarium otherwise . . . . (11)
11. A. Vitellarium 6–8 (occasionally twice this number) oval to digitiform lobes, often arranged in rosette, occasionally branched; Manter's organ absent; pharynx oval
                                                        LECITHASTERIDAE (p. 101)
    B. Vitellarium tubular (filamentous) . . . . (12)
12. A. Manter's organ present; pharynx oval . . . . **SCLERODISTOMIDAE** (p. 111)
    B. Manter's organ absent; pharynx with narrow anterior extension into base of oral sucker; occasionally present on gills; commonly parasitic in sunfish (Molidae)
                                                        ACCACOELIIDAE (p. 57)

13. A. Parasitic in swim-bladder; vitellarium 6–8 oval to digitiform lobes, 2 compact multilobu-
late masses or 2 acinous groups of follicles . . . . **DICTYSARCIDAE** (p. 81)
B. Parasitic in gall-bladder; vitellarium tubular, dendritic, with anteriorly and posteriorly
oriented main collecting ducts situated medially . **SCLERODISTOMOIDIDAE** (p. 114)

Family **ACCACOELIIDAE** Odhner, 1911

Body large or small, commonly elongate. Ecsoma absent. Body-surface smooth, but forebody
may be papillate. Oral and ventral suckers well developed. Ventral sucker normally in anterior
half of body; may be pedunculate. Pharynx well developed; with narrow anterior extension into
base of oral sucker; occasionally modified posteriorly. Oesophagus usually long, occasionally
short. 'Drüsenmagen' present. Gut-caeca usually H-shaped; terminate blindly or more commonly
form uroproct. Testes two; oblique or in tandem; in hindbody, normally close to middle of body;
pre-ovarian. Seminal vesicle thin-walled; tubular; sinuous or convoluted; commonly reaching
into hindbody. Pars prostatica tubular; external gland-cells may be delimited. Short ejaculatory
duct commonly present within sinus-sac. Hermaphroditic duct present or absent. Sinus-sac and
sinus-organ present or absent. Genital atrium present. Ovary oval; post-testicular. Mehlis' gland
pre- or post-ovarian; linked to anterior or posterior region of ovary by oviduct. Laurer's canal
and uterine seminal receptacle present. Juel's organ and canalicular or blind seminal receptacle
absent. Uterus extensive; coils entirely or almost entirely in hindbody; usually passes close to
posterior extremity before looping forward again. Eggs numerous; small; non-filamented.
Vitellarium with one or two main collecting ducts; composed of numerous filamentous tubules
(? or occasionally chains of follicles) in various parts of the fore- or hindbody. Excretory vesicle
Y-shaped; arms initially in dorsal and ventral fields, united in forebody. Metacercariae usually in
coelenterates or ctenophores. Parasitic in gut or occasionally on gills of marine teleosts.

COMMENT The vitellarium of the Paraccacladiinae is typical of many of the primitive hemiuroids,
possessing a symmetrical pair of main collecting ducts which branch distally and unite proximally
to form a common collecting duct. In the Accacoeliinae, however, it appears that the right half of
the vitelline system is reduced to a small vestigial process (or reservoir). The whole of the vitelline
system of the latter group, therefore, corresponds to only the left-hand side of the vitellarium in
other hemiuroids.

Key to Accacoeliidae

1. A. Oesophagus long and narrow; gut-caeca H-shaped; uroproct present; Mehlis' gland pre-
ovarian, linked to anterior region of ovary by oviduct; vitellarium with single main
collecting duct and system of branching tubules . . **ACCACOELIINAE** (p. 57)
B. Oesophagus short; gut-caeca not distinctly H-shaped and end blindly; Mehlis' gland post-
ovarian, linked to posterior region of ovary by oviduct; vitellarium with symmetrical
pair of collecting ducts and system of branching tubules . **PARACCACLADIINAE** (p. 59)

Subfamily **ACCACOELIINAE** Odhner, 1911

Tetrochetinae Looss, 1912, emend. Dollfus, 1935
Accacladiinae Yamaguti, 1958
Orophocotylinae Yamaguti, 1958
Rhynchopharynginae Yamaguti, 1958
Guschanskianinae Skrjabin, 1959

Body usually elongate. Body-surface smooth, but forebody may be papillate. Lateral flanges
occasionally present on ventral sucker. Pharynx occasionally modified to form two muscular
bulbs (*Rhynchopharynx*). Oesophagus long and thin. Gut caeca H-shaped. Uroproct present.
Sinus-sac and sinus-organ present or absent; sinus-sac well or poorly developed when present.
Mehlis' gland pre-ovarian; linked by oviduct to anterior region of ovary. Vitellarium filamentous;
with single main collecting duct on right and single system of ramifying branches in fore- or
hindbody; left-hand system reduced to small process or small ramifying system. Parasitic on
gills or in gut of marine teleosts (especially Molidae).

Key to Accacoeliinae

1. A. Well-defined sinus-sac and sinus-organ present . . . . (2)
   B. Well-defined sinus-sac and sinus-organ absent . . . . (5)
2. A. Ectoparasitic on gills; long proboscis-like sinus-organ; strongly developed ventral muscu-
       lature in hindbody; enormous pars prostatica occupying much of forebody; vitellarium
       posterior to anterior testis . . . . ***ACCACOELIUM***
   B. Endoparasitic in gut; short cylindrical or dome-shaped sinus-organ; vitellarium not
       usually extending posteriorly to ovary . . . . (3)
3. A. Pharynx pyriform with anterior extension into base of oral sucker . . . . (4)
   B. Pharynx with two bulbs and anterior elongate portion ensheathed in glandular posterior
       process of oral sucker; glandular oesophageal bulb immediately posterior to pharynx;
       large glandular organ of unknown function at base of peduncle ***RHYNCHOPHARYNX***
4. A. Vitellarium confined to hindbody; ventral sucker on extensible peduncle; pars prostatica
       relatively short . . . . ***ACCACLADIUM***
   B. Vitellarium wholly or partly in forebody; ventral sucker sessile or nearly so; pars
       prostatica long . . . . ***ACCACLADOCOELIUM***
5. A. Diffuse muscular region around metraterm; muscular sucker-like pads on antero-dorsal
       surface . . . . ***ODHNERIUM***
   B. No sinus-sac detectable; no muscular pads present on antero-dorsal surface . . (6)
6. A. Vitellarium a tubular branching structure on either side of hindbody; no flange on ventral
       sucker . . . . ***TETROCHETUS***
   B. Vitellarium comprising (?) few follicles in four rows between the anterior testis and the
       base of the peduncle; small flange on ventral sucker . . . ***OROPHOCOTYLE***

ACCACOELIUM Monticelli, 1893 [t(w,s)]

Forebody papillate. Oesophagus reaches to ventral sucker. Ventral sucker on short peduncle. Thick muscular layer in ventral hindbody. Sinus-sac present surrounding base of genital atrium. Sinus-organ long and strongly muscular, frequently extended through genital pore. Enormous pars prostatica and associated gland-cells occupy much of forebody. Vitellarium posterior to anterior testis. Parasitic on gills of marine teleosts (*Mola*).

TYPE-SPECIES. *Accacoelium contortum* (Rudolphi, 1819) [by subsequent designation: Looss, 1899].

ACCACLADIUM Odhner, 1928 [t(w,s)]

Body-surface smooth. Oesophagus reaches to ventral sucker. Ventral sucker on extensible peduncle. Pars prostatica well developed. Sinus-sac surrounding base of genital atrium. Sinus-organ short, cylindrical. Vitellarium between ventral sucker and ovary. Parasitic in intestine of marine teleosts (*Mola*).

TYPE-SPECIES. *Accacladium serpentulus* Odhner, 1928 [by original designation].

ACCACLADOCOELIUM Odhner, 1928 [t(w,s); n(w,s)]

Guschanskiana Skrjabin, 1959

Body smooth. Lateral flanges on ventral sucker present or absent. Oesophagus reaches to ventral sucker. Pars prostatica long. Sinus-sac present surrounding base of genital atrium. Sinus-organ short, cylindrical. Vitellarium reaches anteriorly to oral sucker, may extend posteriorly just past ovary but usually not beyond anterior testis; reduced fraction may branch. Parasitic in intestine of marine teleosts (*Mola*).

TYPE-SPECIES. *Accacladocoelium nigroflavum* (Rudolphi, 1819) [by original designation].

ODHNERIUM Yamaguti, 1934 [t(w,s)]

Mneiodhneria Dollfus, 1935
Caballeriana Skrjabin & Guschanskaja, 1959

Body-surface smooth, but with muscular sucker-like pads on antero-dorsal surface. Flange-like muscular extensions present on ventral sucker; latter pedunculate. Oesophagus reaches to ventral sucker. Pars prostatica reaches half-way back to ventral sucker. Diffuse muscular region surrounds distal parts of metraterm and genital atrium (may be vestige of sinus-sac). Male duct enters genital atrium from side through small papilla. Vitellarium tubular, extending from pharynx to ovary. Parasitic in intestine of marine teleosts (*Mola*).

TYPE-SPECIES. *Odhnerium calyptrocotyle* (Monticelli, 1893) [by original designation].

COMMENT. We are using the appellation *Odhnerium* rather than *Mneiodhneria*, despite its similarity to *Odhneria* Travassos, 1921, in accordance with the International Code of Zoological Nomenclature.

OROPHOCOTYLE Looss, 1902

[Inadequately described.] Body-surface smooth. Ventral sucker pedunculate; bears small flange. Oesophagus not reaching to ventral sucker. Pars prostatica short. Sinus-sac not reported. Sinus-organ absent. Vitellarium reported to consist of few (?) follicles in four rows between testes and ventral sucker. Parasitic in intestine of marine teleosts (*Ranzania*).

TYPE-SPECIES. *Orophocotyle planci* (Stossich, 1899) [by original designation].

RHYNCHOPHARYNX Odhner, 1928   [t(w,s)]

Forebody papillate. Ventral sucker pedunculate. Pharynx consisting of two muscular bulbs [the 'pharynx-proper' and the 'Russelblase' (snout-bladder)] and an extended anterior snout ('Russel'), which may be extended through the oral sucker. Oral sucker possesses posterior glandular extension, the snout-sheath ('Russelscheide'), which envelopes the snout. Glandular oesophageal bulb present immediately posterior to pharynx. Oesophagus reaches to ventral sucker. Large glandular organ of unknown function present at base of peduncle. Pars prostatica long. Sinus-sac surrounds base of genital atrium. Sinus-organ small. Vitellarium extends from anterior region of ventral sucker to ovary. Parasitic in intestine of marine teleosts (*Mola*).

TYPE-SPECIES. *Rhynchopharynx paradoxa* Odhner, 1928 [by original designation].

TETROCHETUS Looss, 1912   [t(w,s); n(w,s)]

Paratetrochetus Hanson, 1955

Body-surface smooth. Ventral sucker pedunculate. Oesophagus long. Diverticula present at intestinal bifurcation. Pars prostatica short, straight, narrow. Sinus-sac and sinus-organ absent. Male and female ducts open together into shallow genital atrium. Vitellarium tubular, in hind-body; reduced half may be branched. Parasitic in intestine of medusophagus and carnivorous marine teleosts.

TYPE-SPECIES. *Tetrochetus raynerii* (Nardo, 1833) [by monotypy].

Subfamily PARACCACLADIINAE Bray & Gibson, 1977

Body elongate. Body-surface smooth, but with papillae on outer surface of ventral sucker. Ventral sucker on short peduncle. Pharynx extended into base of oral sucker. Oesophagus short, wide. Anterior caecal shoulders small. Gut-caeca terminate blindly near posterior extremity. Pars prostatica elongate, convoluted. Sinus-sac present surrounding base of genital atrium; musculature diffuse. Sinus-organ short, cylindrical. Mehlis' gland post-ovarian; linked to posterior region of ovary by oviduct. Vitellarium with symmetrical pair of main collecting ducts and ramifying systems of tubules; posterior to ovary. Mature forms parasitic in rectum of carnivorous marine teleosts (*Coryphaenoides*); immature forms parasitic in rectum of medusophagus marine teleosts.

PARACCACLADIUM Bray & Gibson, 1977   [T(w,s)]

Defined as subfamily.

TYPE-SPECIES. *Paraccacladium jamiesoni* Bray & Gibson, 1977 [by original designation].

Family AZYGIIDAE Lühe, 1909

Aphanhysteridae Guiart, 1938

Body large or small; usually elongate. Ecsoma absent. Body-surface smooth, without spines or plications. Oral and ventral suckers well developed; latter in middle or anterior half of body. Prepharynx absent. Pharynx well developed. Oesophagus usually short. 'Drüsenmagen' apparently absent. Gut-caeca terminate blindly close to posterior extremity. Testes two; in tandem, oblique or symmetrical; pre- or post-ovarian in hindbody. Seminal vesicle tubular, usually short, thin-walled; convoluted in forebody. Pars prostatica tubular. Prostatic sac present surrounding pars prostatica and seminal vesicle. Ejaculatory duct usually long and convoluted, but of variable length. Hermaphroditic duct short; at distal extremity of sinus-organ. Permanent sinus-organ variable in length; usually conical. Sinus-sac absent. Genital atrium usually well developed; variable in size. Genital pore mid-ventral in forebody. Ovary oval; pre- or post-testicular. Mehlis' gland pre-ovarian. Laurer's canal and uterine seminal receptacle present. Juel's organ and canalicular or blind seminal receptacle absent. Uterus entirely or almost entirely pre-ovarian; coiled mainly in hindbody. Eggs numerous; small; non-filamented. Vitellarium follicular; usually present laterally throughout much of hindbody; occasionally extending into forebody. Excretory vesicle Y-shaped; arms united in forebody or not. Parasitic in stomach or body-cavity of elasmobranchs and in stomach of freshwater teleosts and holosteans.

Key to Azygiidae

1. A. Testes post-ovarian.   .   .   .   .   **AZYGIINAE** (p. 60)
   B. Testes pre-ovarian .   .   .   .   **LEUCERUTHRINAE** (p. 62)

Subfamily AZYGIINAE Lühe, 1909

Aphanhysterinae Guiart, 1938
Gomtiotrematinae Gupta, 1955
Allogomtiotrematinae Yamaguti, 1958
Proterometrinae Yamaguti, 1958

Body normally large; occasionally small. Ventral sucker larger or smaller than oral sucker; in middle or anterior half of body. Testes in tandem, oblique or symmetrical; post-ovarian. Uterus entirely pre-testicular. Vitelline field may extend into forebody. Excretory arms may or may not unite in forebody. Parasitic in stomach or body-cavity of elasmobranchs and stomach of freshwater teleosts and holosteans.

Key to Azygiinae

1. A. Testes symmetrical; vitelline follicles and uterine coils extending into forebody; testes near posterior extremity; in freshwater teleosts (N. America)   .   .   .   *PROTEROMETRA*
   B. Testes tandem, oblique, or occasionally symmetrical; vitelline follicles and uterine coils entirely or almost entirely confined to hindbody; testes usually well anterior to posterior extremity   2
2. A. Vitelline follicles confluent posterior to testes; ventral sucker normally larger than oral sucker; parasitic in elasmobranchs.   .   .   .   .   .   .   *OTODISTOMUM*
   B. Vitelline follicles not confluent posterior to testes; oral sucker normally larger than ventral sucker; parasitic in freshwater teleosts and holosteans   .   .   .   .   .   *AZYGIA*

AZYGIA Looss, 1899 [t(w,s)]

Megadistomum Stafford, 1904
Mimodistomum Stafford, 1904
Hassallius Goldberger, 1911
Eurostomum MacCallum, 1921
Gomtiotrema Gupta, 1955, *nec* Sinha, 1934
Allogomtiotrema Yamaguti, 1958

Body medium to large; usually elongate, occasionally oval. Ventral sucker smaller than oral sucker; in anterior half of body. Testes tandem, occasionally to symmetrical; anterior testis occasionally lateral to ovary (*A. asiatica*). Sinus-organ a small papilla-like structure. Uterine field between ovary and ventral sucker. Vitelline follicles confined to hindbody; not confluent posterior to testes. Excretory arms apparently not united in forebody. Parasitic in stomach and intestine of freshwater teleosts and holosteans.

TYPE-SPECIES. *Azygia lucii* (Müller, 1776) [by subsequent designation: Goldberger, 1911a].

COMMENT. Yamaguti (1971) recognizes two subgenera, *Azygia* Looss, 1899, and *Pseudazygia* Yamaguti, 1971. He distinguishes these by the length of the post-testicular region and the position of the bifurcation of the excretory vesicle. The former criterion appears to be a somewhat variable feature in *Azygia asiatica* Simha & Pershad, 1964, and in *A. angusticauda* (Stafford) of Kakaji (1968; ? synonym of *A. asiatica*).

OTODISTOMUM Stafford, 1904 [t(w,s); n(w,s)]

Xenodistomum Stafford, 1904
Josstaffordia Odhner, 1911*
Aphanhystera Guiart, 1938

Body large; spatulate to elongate. Ventral sucker larger than oral sucker; close to anterior extremity. Testes tandem or slightly oblique. Sinus-organ capable of considerable extension or contraction to form small papilla. Uterine field almost entirely between ovary and ventral sucker. Vitelline follicles extend in lateral fields posterior to ventral sucker, reaching back to post-testicular region where fields are confluent. Excretory arms usually unite in forebody, but occasionally do not. Parasitic in stomach or body-cavity of elasmobranchs (sharks, rays and chimaeras).

TYPE-SPECIES. *Otodistomum veliporum* (Creplin, 1837) [by monotypy].

COMMENT. It is worth noting that there are two body-forms present in this genus, which appear to be related to their location within the host. The species parasitic within the body-cavity tend to be broad or spatulate, whilst those parasitic in the stomach are very elongate. It is possible that the spatulate body-shape has been evolved to prevent these parasites being lost through the abdominal pores, and it is noticeable that the gorgoderid and monogenean parasites from the body-cavity of elasmobranchs are also spatulate or oval. Elasmobranchs are the only group of vertebrates which commonly harbour adult helminths in the body-cavity: this is because the abdominal pores form an exit for the release of eggs. The excretory arms in species of *Otodistomum* are normally considered to unite in the forebody; but in sectioned material of *O. plunketi* Fyfe, 1953, they end blindly (Gibson & Bray, 1977).

PROTEROMETRA Horsfall, 1933

Body oval; small. Oral sucker large; ventral sucker small, situated at or just posterior to middle of body. Testes symmetrical at posterior extremity. Sinus-organ a small cone. Uterine field extends from ovary into forebody. Vitellarium extends from level of testes or ovary anteriorly

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* The appellation *Josstaffordia josstaffordi* n.g., n.sp. was proposed by Odhner (1911) for specimens of *Otodistomum* in a sarcastic footnote, mimicking the erection of *Hassallius hassalli* by Goldberger (1911a). Although he gives indications as to its distinctive features, it is obvious that Odhner did not intend it to be considered valid.

well into forebody, in lateral fields. Excretory arms united in forebody. Parasitic in gut of fresh-water teleosts (in North America).

TYPE-SPECIES. *Proterometra macrostoma* (Faust, 1918) [by monotypy].

Subfamily LEUCERUTHRINAE Goldberger, 1911

Body medium to large; elongate oval. Ventral sucker smaller than oral sucker; near middle of body. Testes oblique; pre-ovarian; immediately posterior to ventral sucker. Prostatic sac small. Sinus-organ small, but well defined. Uterine field between ovary and ventral sucker, passing between testes. Vitelline follicles in lateral fields, extending almost throughout length of hindbody. Excretory arms unite in forebody. Parasitic in gut of freshwater teleosts and holosteans (in North America).

LEUCERUTHRUS Marshall & Gilbert, 1905

Defined as subfamily.

TYPE-SPECIES. *Leuceruthrus micropteri* Marshall & Gilbert, 1905 [by monotypy].

Family BATHYCOTYLIDAE Dollfus, 1932

Body large; elongate, but stout. Ecsoma absent. Body-surface smooth, but may be wrinkled. Oral and ventral suckers well developed; latter just in anterior half of body. Pharynx well developed. Oesophagus short. 'Drüsenmagen' present. Gut-caeca end blindly close to posterior extremity. Testes two; tandem; separated by ovary; in mid-hindbody. Seminal vesicle thin-walled; tubular; convoluted; small; well forward in forebody. Pars prostatica tubular; indistinct. Sinus-organ and sinus-sac absent. Genital atrium small, but deep. Genital pore mid-ventral close to posterior margin of oral sucker. Ovary oval to reniform; inter-testicular. Mehlis' gland posterior or lateral to ovary. Laurer's canal [see below] and uterine seminal receptacle present. Juel's organ and canalicular or blind seminal receptacle absent. Uterus fills much of hind- and forebody. Eggs numerous; small; non-filamented. Vitellarium several filamentous tubules in hindbody. Excretory vesicle Y-shaped; arms united in forebody. Parasitic on gills (? or in stomach) of pelagic marine teleosts (scombrids and *Coryphaena*).

BATHYCOTYLE Darr, 1902 [n(w,s)]

Defined as family.

TYPE-SPECIES. *Bathycotyle branchialis* Darr, 1902 [by monotypy].

COMMENT. Although Yamaguti (1938a) states: 'Laurer's canal apparently without external opening', when describing *Bathycotyle coryphaenae* Yamaguti, 1938, it is obvious that a dorsal pore does occur in the type-species, as Dollfus (1932) clearly illustrated it in his figure 5. Yamaguti, however, in contrast to Dollfus, apparently failed to section his material.

Family BUNOCOTYLIDAE Dollfus, 1950

Body usually small; fusiform to elongate. Distinct ecsoma absent, but vestige may remain. Body-surface smooth or with plications. Ridges around body often present at level of oral sucker and posterior margin of ventral sucker. Ventral sucker normally inside anterior half of worm. Pharynx well developed. Oesophagus normally short. 'Drüsenmagen' normally present. Gut-caeca normally end blindly near posterior extremity or occasionally form cyclocoel. Testes two; pre-ovarian in hindbody; tandem to symmetrical. Seminal vesicle saccular or tubular; in fore- or hindbody. Pars prostatica tubular or vesicular; short or long; may extend into hindbody. Ejaculatory duct long, short or apparently absent. Sinus-sac usually present, occasionally absent. Hermaphroditic duct present; within sinus-sac when latter present. Permanent sinus-organ

normally absent, but temporary sinus-organ may form. Genital atrium small or absent. Ovary oval; rarely bilobed; between testes and vitellarium. Mehlis' gland post-ovarian. Laurer's canal and canalicular seminal receptacle absent. Juel's organ and uterine seminal receptacle present or absent. Blind seminal receptacle present or absent. Uterus normally almost entirely in hindbody; mainly pre- to mainly post-ovarian. Eggs numerous; small; without filaments. Vitellarium one or two, occasionally three, entire (rarely slightly lobed) masses; posterior or postero-lateral to ovary. Excretory arms rarely fail to unite in forebody; stem of excretory vesicle often with terminal bulb or with large pore (actual pore may be withdrawn within vestige of ecsoma). Parasitic mainly in stomach of marine teleosts.

Key to Bunocotylidae

1. A. Uterine seminal receptacle present; vitellarium 1 or 2 masses 2
   B. Blind seminal receptacle present; body-surface smooth; vitellarium 2 or 3 masses
      OPISTHADENINAE (p. 66)
2. A. Parasites up to 6 mm in length; large concentration of uterine coils between ovary and testes . . . . **THELETRINAE** (p. 69)
   B. Parasites small, rarely more than 2 mm in length, commonly less than 1 mm; large concentration of uterine coils not present between ovary and testes 3
3. A. Body-surface smooth; ridges present around body at level of oral sucker and posterior margin of ventral sucker; major part of uterine field pre-ovarian; vitellarium single
      BUNOCOTYLINAE (p. 63)
   B. Body-surface usually plicated, occasionally smooth; ridges around body at level of sucker absent; large or major part of uterine field post-ovarian; vitellarium single or double
      APHANURINAE (p. 64)

Subfamily **BUNOCOTYLINAE** Dollfus, 1950

Body small. Vestige of ecsoma may be present. Body-surface smooth. Ridges present around body at level of oral sucker and posterior margin of ventral sucker; additional ridge often present close to posterior extremity. Transverse septate partitions of body may occur. Gut-caeca end blindly or form cyclocoel. Testes tandem to oblique; not separated from ovary by large concentration of uterine coils. Seminal vesicle saccular; oval to elongate; in forebody or dorsal to ventral sucker. Pars prostatica short; tubular or vesicular. Sinus-sac absent or small and tubular to oval. Short hermaphroditic duct may extend to form temporary sinus-organ. Genital atrium absent or small. Ovary oval. Uterine seminal receptacle present (?). Juel's organ not reported. Blind seminal receptacle absent. Vitellarium a single, unlobed mass; immediately post-ovarian. Excretory vesicle expanded distally; arms united in forebody; pore wide. Parasitic in gut of freshwater and euryhaline teleosts; occasionally progenetic in snails and copepods.

COMMENT. According to the literature, the type of seminal storage apparatus occurring in this subfamily is a matter of some disagreement. Manter (1969a) observed a uterine seminal receptacle in *Saturnius segmentatus* Manter, 1969, whereas Yamaguti (1970) described a seminal receptacle in *S. mugilis* (Yamaguti, 1970). Overstreet (1977), when re-defining *Saturnius*, stated that a seminal receptacle was absent. No seminal storage apparatus has been described for *Bunocotyle cingulata* Odhner, 1928, by Odhner (1928b) or for *B. progenetica* (Markowski, 1936) by Deblock (1975). We have examined sections of a paratype specimen of *Saturnius papernai* Overstreet 1977, and confirm that: (1) a distinct seminal receptacle (canalicular or blind) and Laurer's canal are absent; and (2) spermatozoa are present in the proximal region of the uterus, which thus functions as a uterine seminal receptacle. We could not for certain distinguish Juel's organ, but it is possible that in the small species which constitute this subfamily, this structure is reduced or lost altogether.

It is conceivable that the transverse ridge around the posterior extremity in some species of this subfamily, and possibly both the ampullaceous nature of the distal region of the stem of the excretory vesicle and the wide excretory pore, represent vestiges of an ecsoma. Overstreet (1977) has described the former as a possible small ecsoma in *S. maurepasi* Overstreet, 1977, where, in the living worm, it may be partly withdrawn.

Key to Bunocotylinae

1. A. Transverse fibrous septa in fore- and hindbody; cyclocoel absent; sinus-sac present; parasitic in euryhaline teleosts *(Mugil)* . . . . *SATURNIUS*

   B. Transverse septa not present; cyclocoel present; sinus-sac absent; parasitic in freshwater or euryhaline teleosts, or progenetic in snails and copepods . . *BUNOCOTYLE*

BUNOCOTYLE Odhner, 1928

Transverse fibrous septa absent. Cyclocoel present. Sinus-sac absent. Uterine seminal receptacle (?) presumed to be present. Parasitic in gut of freshwater or euryhaline teleosts, or progenetic in snails and copepods.

TYPE-SPECIES. *Bunocotyle cingulata* Odhner, 1928 [by original designation].

COMMENT. See *Theletrum* for comment on *B. sudatlantica* Parukhin, 1976.

SATURNIUS Manter, 1969 [n(w,s)]

Small papillae or corrugations may be associated with suckers. Internal transverse, fibrous septa present in fore- and hindbody. Gut-caeca end blindly. Sinus-sac may contain ejaculatory (? hermaphroditic) vesicle. Parasitic in, and under lining of, stomach of euryhaline teleosts (*Mugil cephalus*).

TYPE-SPECIES. *Saturnius segmentatus* Manter, 1969 [by original designation].

COMMENT. This genus has recently been revised by Overstreet (1977), who has cleared up many of the discrepancies between the descriptions of *S. segmentatus* and *S. mugilis* (Yamaguti, 1970).

Subfamily **APHANURINAE** Skrjabin & Guschanskaja, 1954 [28.4.1954]

Ahemiurinae Chauhan, 1954 [17.11.1954]

Body normally small. Vestige of ecsoma may be present. Body-surface usually with distinct annular plications, occasionally (?) smooth [some species of *Aphanurus*]. Ridges around body at level of suckers absent. Gut-caeca end blindly near posterior extremity. Testes tandem to symmetrical; normally well posterior to ventral sucker; not separated from ovary by large concentration of uterine coils. Seminal vesicle tubular in forebody, or saccular (oval, elongate or bipartite) in hindbody (or at least posterior to middle of ventral sucker). Pars prostatica tubular or vesicular; short or long. Ejaculatory duct long, short or apparently absent. Sinus-sac present, enclosing hermaphroditic duct, or (?) absent. Ovary oval; immediately or almost immediately post-testicular. Blind seminal receptacle absent. Uterine seminal receptacle and (?) Juel's organ present. Large or major part of uterine field post-ovarian. Vitellarium one or two compact masses; usually immediately posterior, occasionally lateral, to ovary. Excretory arms united in forebody; excretory pore often large; actual pore may be withdrawn within vestige of ecsoma. Parasitic mainly in stomach or oesophagus of marine teleosts.

COMMENT. A small 'seminal receptacle' has been reported for *Duosphincter* by Yamaguti (1970) and in some species of *Aphanurus*. A uterine seminal receptacle has been reported for *Myosaccium* and other species of *Aphanurus*. It is likely that the reports of a 'seminal receptacle' from this group are mistaken, as Juel's organ and a uterine seminal receptacle are easily mistaken for such a structure in whole-mount preparations.

The genera of this group are essentially typical hemiurids which have lost their ecsoma. The presence of records from the oesophagus suggests that these parasites may inhabit the less acidic anterior regions of the stomach, and do not have the same requirement for an ecsoma as the closely related forms which tend to inhabit the pyloric region of the stomach.

Key to Aphanurinae

1. A. Vitellarium composed of 2 distinct masses 2
   B. Vitellarium composed of 1 distinct mass . . . . . . *APHANURUS*
2. A. Seminal vesicle tubular, winding in forebody . . . . . *DUOSPHINCTER*
   B. Seminal vesicle saccular (oval, elongate or bipartite; often attenuated anteriorly), posterior
       to middle of ventral sucker 3
3. A. Pars prostatica vesicular, with muscular wall . . . . . *MYOSACCIUM*
   B. Pars prostatica tubular 4
4. A. Seminal vesicle oval; sinus-sac present . . . . *AHEMIURUS*
   B. Seminal vesicle apparently bipartite and attenuated anteriorly; sinus-sac apparently absent
                                                              APHANUROIDES

APHANURUS Looss, 1907   [n(w)]

Chauhanurus Skrjabin & Guschanskaja, 1954
Helaphanurus Slusarski, 1957

Body-surface normally plicated, occasionally (?) smooth. Testes oblique, occasionally symmetrical or tandem. Seminal vesicle oval to elongate oval; in hindbody; wall may be muscular. Pars prostatica tubular; long. Ejaculatory duct long or short. Sinus-sac present; tubular. Temporary sinus-organ sometimes present as small cone. Vitellarium a single, large, entire or slightly indented, post-ovarian mass. Parasitic in oesophagus and stomach of essentially marine teleosts from marine and brackish water environments.

TYPE-SPECIES. *Aphanurus stossichi* (Monticelli, 1891) [by original designation].

COMMENT. There has been considerable comment in the literature (Looss, 1908; Rioja, 1923; Chauhan, 1954; Slusarski, 1957) as to whether *Aphanurus* possesses or lacks a small vestigial ecsoma. Although this question has not been resolved, Chauhan (1954) suggested that the confusion may have been caused by the bulbous nature of the excretory vesicle. The possible vestiges of an ecsoma, however, may be a common feature of both the aphanurines and the bunocotylines. Some species of *Aphanurus* (*A. caesionis* Yamaguti, 1952 and *A. dorosomatis* Yamaguti, 1953) are reported to have a smooth body-surface; but, as they are known from only one or two specimens, this requires confirmation. If this is proved to be correct, then there may be grounds for distinguishing them from the other species of *Aphanurus* at the generic level.

AHEMIURUS Chauhan, 1954

Testes symmetrical to oblique. Seminal vesicle oval; in hindbody. Pars prostatica tubular; long. Ejaculatory duct long. Sinus-sac present; elongate oval. Vitellarium two oval, compact masses; symmetrical; post-ovarian. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Ahemiurus karachii* (Srivastava, 1937) [by original designation].

COMMENT. Yamaguti (1971) lists *Ahemiurus* as a synonym of *Opisthadena* despite the fact that Chauhan (1954) emphasized the presence of cuticular plications in this species. The latter is a feature which occurs only in hemiurid and aphanurine genera. Although the seminal storage apparatus of the genus has not been described, we expect it to conform to the subfamily definition.

(?) *APHANUROIDES* Nagaty & Abdel-Aal, 1962

[Inadequately described.] Testes tandem. Seminal vesicle saccular; (?)bipartite; attenuated anteriorly; extending between anterior testis and posterior half of ventral sucker. Pars prostatica tubular. [Terminal genitalia not described in detail.] Sinus-sac (?) absent. Short hermaphroditic duct and genital atrium apparently present. [Figures of Nagaty & Abdel-Aal, 1962, suggest that temporary sinus-organ may form (?).] Vitellarium two compact masses; symmetrical to oblique; post-ovarian. Excretory arms (?). Parasitic in gut of marine teleosts.

TYPE-SPECIES: *Aphanuroides lethrini* Nagaty & Abdel-Aal, 1962 [by original designation].

DUOSPHINCTER Manter & Pritchard, 1960

Strongly developed sphincter muscles surround apertures of suckers. Testes oblique to tandem. Seminal vesicle tubular; winding in forebody. Pars prostatica tubular; short. Sinus-sac small; oval. Temporary sinus-organ may form. [Small seminal receptacle (? Juel's organ) present, according to Yamaguti, 1970.] Vitellarium two oval masses; oblique to tandem; immediately post-ovarian. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Duosphincter zancli* Manter & Pritchard, 1960 [by monotypy].

MYOSACCIUM Montgomery, 1957

Neogenolinea Siddiqi & Cable, 1960.

Testes symmetrical to tandem. Seminal vesicle saccular; attenuated anteriorly; at level of posterior margin of ventral sucker. Pars prostatica vesicular; with strong, muscular wall; in forebody. [Terminal genitalia confused in literature.] Sinus-sac apparently tubular; enclosing hermaphroditic duct, which may form temporary sinus-organ. Eggs without filament [the structure of collapsed eggs may apparently give the impression that a short filament and spine are present (?)]. Vitellarium two oval or slightly indented masses; oblique to tandem; one mass usually lateral, other immediately postero-lateral or posterior, to ovary. Parasitic in stomach of marine teleosts (Clupeidae).

TYPE-SPECIES. *Myosaccium ecaude* Montgomery, 1957 [by original designation].

COMMENT. There appears to be some difference of opinion with regard to the presence or absence of filaments on the eggs. Montgomery (1957) and Kohn & Bührnheim (1964) indicate that a filament is present with, in the case of the latter authors, an additional small spine at the opposite end of the egg. Overstreet (1969) and Yamaguti (1971), after examining some of Montgomery's type-specimens, state that filaments on the egg could not be seen. Overstreet suggests that the so-called filaments described in this genus may be an artifact present in collapsed eggs.

Subfamily **OPISTHADENINAE** Yamaguti, 1970

Intuscirrinae Skrjabin & Guschanskaja, 1959

Body spindle-shaped to elongate. Body-surface smooth. Transverse ridges in body-wall present or absent around body at level of oral sucker and/or posterior margin of ventral sucker [these are often not obvious]. Presomatic pit reported (?) in *Mitrostoma*. Gut-caeca end blindly near posterior extremity. Testes tandem to oblique; usually well posterior to ventral sucker and near ovary; not separated from ovary by large concentration of uterine coils. Seminal vesicle tubular to saccular (? rarely bipartite); in fore- or hindbody. Pars prostatica long or short; tubular or vesicular. Ejaculatory duct long to short or apparently absent. Sinus-sac present; oval to elongate oval; enclosing hermaphroditic duct. Sinus-organ (? temporary) occasionally present. Genital atrium usually present; small. Ovary normally oval, occasionally bilobed; normally close to testes. Blind seminal receptacle present; large; usually dorsal or antero-dorsal to ovary. Juel's organ and uterine seminal receptacle absent. Uterus mainly pre- to mainly post-ovarian. Vitellarium two, occasionally three, entire or slightly indented masses; posterior or postero-lateral to ovary. Excretory arms usually, but not always, united in forebody. Parasitic in stomach, occasionally intestine, of marine teleosts.

COMMENT. The presence of ridges (tegumental folds) around the body, especially the one immediately posterior to the ventral sucker, may well be a good generic criterion. We are concerned about the significance of this feature, as it is often very difficult to see, and in genera such as *Genolinea*, where it is known to occur, it has only been reported occasionally.

Key to Opisthadeninae

1. A. Seminal vesicle entirely in hindbody 2
   B. Seminal vesicle in forebody (occasionally dorsal or postero-dorsal to ventral sucker) . 3
2. A. Ejaculatory duct short or absent; pars prostatica reaches forward to level of caecal bifurcation; (?) presomatic pit apparently present . . . . . . *MITROSTOMA*
   B. Ejaculatory duct long; pars prostatica does not reach further forward than ventral sucker; presomatic pit absent . . . . *OPISTHADENA*
3. A. Vitellarium 2 symmetrical, oblique or tandem masses . . . . . *GENOLINEA*
   B. Vitellarium 3 masses, the anterior pair being symmetrical and the posterior mass being the largest . . . . *NEOTHELETRUM*

OPISTHADENA Linton, 1910

Body elongate. Transverse ridge (fold) of body-wall around body immediately posterior to ventral sucker. Testes tandem; posterior to middle of body. Seminal vesicle in hindbody; usually tubular and sinuous, but reported as enclosed within muscular, ovoid sac ['seminal sac' of Manter, 1947] or as being saccular. Pars prostatica tubular; not reaching further forward than posterior margin of ventral sucker. Ejaculatory duct long. Sinus-sac oval. Hermaphroditic duct may be sub-divided. Sinus-organ apparently present as small cone, at least temporarily. Ovary close to testes. Uterus mainly pre-ovarian. Vitellarium two symmetrical to oblique masses; post-ovarian. Excretory arms diverticulate; united in forebody. Parasitic in stomach of marine teleosts (especially *Kyphosus*).

TYPE-SPECIES. *Opisthadena dimidia* Linton, 1910 [by original designation].

GENOLINEA Manter, 1925 [t(w,s); n(w,s)]

Parasterrhurus Manter, 1934
Intuscirrus Acena, 1947
Pseudobunocotyla Yamaguti, 1965

Body spindle-shaped to slightly elongate. Transverse ridge usually present around body immediately posterior to ventral sucker (often inconspicuous and frequently not reported); similar ridge may surround oral sucker. Large pre-oral lobe may be present. Ventral sucker normally in anterior half of body, (?) occasionally near middle; sphincter muscles sometimes present around aperture. Testes tandem to oblique; close to ovary. Seminal vesicle small; tubular; convoluted in forebody, occasionally dorsal or postero-dorsal to ventral sucker. Pars prostatica tubular to vesicular; short. Ejaculatory duct short or absent. Sinus-sac oval to elongate oval; small. Sinus-organ occasionally present (? temporary). Ovary near middle of hindbody. Uterus usually in both pre- and post-ovarian fields, occasionally post-vitelline distribution is limited. Metraterm reported in some instances to be spinous (?). Vitellarium two compact (occasionally lobed), symmetrical, oblique or tandem masses; posterior or postero-lateral to ovary. Excretory arms united in forebody. Parasitic mainly in stomach of marine teleosts.

TYPE-SPECIES. *Genolinea laticauda* Manter, 1925 [by original designation].

COMMENT. The position of the ventral sucker near the middle of the body in *G. dactylopagri* Manter, 1954, is much further posterior than normally occurs in this family. The morphology of this species suggests that it is related to *Leurodera* Linton, 1910, as Manter (1954) initially believed, and both are recorded from related percoid families of teleosts.

MITROSTOMA Manter, 1954

Body elongate. Thickened projection present on each side of body at level of posterior margin of ventral sucker. Nipple-shaped protuberance (? vestige of ecsoma) may be present at posterior extremity. Weakly muscled pre-oral lobe bears mouth. Structure resembling (?) presomatic pit apparently present anterior to ventral sucker. Ventral sucker with 'sphincter muscles in anterior and posterior halves'. Testes tandem; close to ovary; near middle of hindbody. Seminal vesicle

tubular; convoluted; entirely in hindbody. Pars prostatica tubular; reaches forward to caecal bifurcation. Ejaculatory duct short or absent. Sinus-sac short; pyriform; (?) protrusible. Ovary in posterior half of hindbody. Uterus mainly pre-ovarian, but does extend into post-vitelline region. Vitellarium two oblique to symmetrical, post-ovarian masses. Excretory arms united in forebody. Parasitic in intestine of marine teleosts.

TYPE-SPECIES. *Mitrostoma nototheniae* Manter, 1954 [by original designation].

COMMENT. There are several features of the genus *Mitrostoma*, such as the overall arrangement of the organs, the apparent presence of a presomatic pit and the reported presence of a nipple-shaped protuberance at the posterior extremity of one specimen, which suggests that it might be a hemiurid with a lost or vestigial ecsoma, no longer required because of its intestinal habitat. Manter (1954), however, reported that a blind seminal receptacle was present. The presence of this type of seminal receptacle, as opposed to a uterine seminal receptacle, and the great morphological similarity between this parasite and *Genolinea bowersi* (Leiper & Atkinson, 1914), reported from related nototheniid hosts (Prudhoe & Bray, 1973), indicate that its position within the Opisthadeninae is probably correct.

NEOTHELETRUM gen. nov.

Body small; elongate to spindle-shaped. Tegumental fold around body posterior to ventral sucker apparently absent. Body-surface smooth. Ventral sucker in anterior half of body. Pre-pharynx absent. Pharynx well developed. Oesophagus short; often with small diverticulum. Gut-caeca end blindly near posterior extremity. Testes 2; oval; oblique to symmetrical; usually separated from ventral sucker by loops of uterus; occasionally sandwiched between ventral sucker and ovary. Seminal vesicle small; tubular to saccular (? occasionally bipartite); in forebody. Pars prostatica short; tubular to vesicular. Ejaculatory duct short or absent. Sinus-sac small; oval. Small temporary sinus-organ may form. Hermaphroditic duct short; formed within sinus-sac. Genital atrium small. Genital pore mid-ventral in forebody. Ovary oval (may occasionally be bilobed); post-testicular; near middle of hindbody. Blind seminal receptacle antero-dorsal to ovary. Laurer's canal, Juel's organ and both canalicular and uterine seminal receptacle presumably absent. Uterus almost entirely in hindbody; usually with roughly equal amounts in pre- and post-ovarian fields; occasionally with majority of uterus in post-ovarian field. Eggs small; numerous; without filaments. Vitellarium three compact, entire or slightly indented masses; anterior pair symmetrical, connected by narrow isthmus; posterior mass larger, may be slightly bilobed [vitellarium is essentially two tandem masses, the anterior of which is divided into two distinct lobes: the vitellarium may appear as two tandem masses in lateral view]; post-ovarian. Excretory arms united in forebody or not. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Neotheletrum lissosomum* (Manter, 1940) n. comb.

COMMENT. *Neotheletrum* differs from *Theletrum* in that: (1) a blind rather than a uterine seminal receptacle is present; (2) much of the uterus is post-ovarian rather than being between the ovary and testes; (3) the anterior vitelline mass is consistently divided into two; and (4) the tegumental ridge around the body immediately posterior to the ventral sucker is absent.

The additional species which we include in this genus are as follows:
> *N. frontilatum* (Manter, 1969) n. comb.
> *N. gravidum* (Manter, 1940) n. comb.
> *N. magnasaccum* (Sogandares-Bernal & Sogandares, 1961) n. comb. [possibly a synonym
> of *N. lissosomum*].
> *N. pomacentri* (Nahhas & Cable, 1964) n. comb.

N. frontilatum, which Yamaguti (1971) considers to belong to *Hysterolecithoides*, differs from the other species of *Neotheletrum* in that the uterus is almost entirely post-ovarian, the testes are close behind the ventral sucker and close to the ovary, and the excretory arms are not united in the forebody. On these grounds a case could be made for erecting a new genus for this species; but we have included it in *Neotheletrum* as there seems little point in further sub-division at present.

THELETRINAE subfam. nov.

Body elongate. Ecsoma absent. Body-surface smooth; papillae may be present ventrally in fore- or hindbody; transverse ridge may be present around body near posterior margin of ventral sucker and possibly around oral sucker. Oral and ventral suckers well developed; ventral sucker in anterior half of body. Prepharynx absent. Pharynx well developed. Oesophagus short. Gut-caeca end blindly near posterior extremity, (?) or at level of ovary. Testes two; pre-ovarian; tandem to oblique; near middle of hindbody; separated from ovary by majority or large part of uterine coils. Seminal vesicle tubular or (?) saccular; in forebody, but sometimes reaching back to posterior margin of ventral sucker. Pars prostatica short; tubular or slightly vesicular. Ejaculatory duct short or apparently absent. Sinus-sac usually small; oval or elongate oval; weakly developed; enclosing hermaphroditic duct; may extrude slightly through genital pore. Permanent sinus-organ absent (?), but temporary sinus-organ may form. Genital atrium small or absent. Ovary oval; near posterior extremity or at least well inside posterior half of hindbody. Laurer's canal and both canalicular or blind seminal receptacle absent [Laurer's canal reported present (?) in *Indoderogenes*]. Uterine seminal receptacle present. Juel's organ assumed to be present. Uterus almost entirely or mainly in hindbody (small part of uterus is coiled in forebody of *Monoleci-thotrema*); mainly pre-ovarian, with large proportion of uterine coils between ovary and testes. Eggs numerous; small; without filaments. Vitellarium one entire or two tandem to oblique, entire or slightly lobed masses; posterior or postero-lateral to ovary. Excretory vesicle Y-shaped; arms united in forebody. Parasitic normally in stomach of marine teleosts.

COMMENT. This subfamily is erected for forms which resemble the Opisthadeninae; but lack a blind seminal receptacle, possess a uterine seminal receptacle (plus presumably Juel's organ) and contain a large concentration of uterine coils between the ovary and testes. The position of *Indoderogenes* Srivastava, 1937, discussed below, is problematical; but in gross morphology it does appear to key satisfactorily to this subfamily.

The sinus-sac in both *Theletrum* and *Monolecithotrema* often appears to be slightly extruded through the genital pore. It is not clear from our observations of the type-species if this is in fact so, or whether a temporary sinus-organ is formed by an eversion of the hermaphroditic duct.

Key to Theletrinae

1. A.   Vitellarium single (great care should be taken with this observation, as at certain angles the vitellarium of *Theletrum* appears to be single); transverse ridge posterior to ventral sucker absent; some uterine coils in forebody .   .   .   . ***MONOLECITHOTREMA***
   B.   Vitellarium double; uterus not coiled in forebody   2
2. A.   Seminal vesicle tubular; transverse ridge normally present posterior to ventral sucker; gut-caeca terminate near posterior extremity .   .   .   .   .   ***THELETRUM***
   B.   Seminal vesicle saccular; transverse ridge posterior to ventral sucker not reported; gut-caeca apparently terminate at level of anterior margin of ovary.   .   ***INDODEROGENES***

THELETRUM Linton, 1910   [t(w)]

Transverse tegumental ridge present around body immediately posterior to ventral sucker and possibly around oral sucker. Papillae may be present ventrally in hindbody. Gut-caeca terminate at posterior extremity. Testes fairly close together, but separated by uterus. Seminal vesicle tubular. Pars prostatica slightly vesicular. Sinus-sac elongate oval; thin-walled; sheath-like; may be partly extruded through genital pore. Ovary close to posterior extremity. Uterine coils entirely or almost entirely in hindbody; few or no coils posterior to vitellarium. Vitellarium two oblique, entire or slightly lobed masses; close together; posterior or postero-lateral to ovary; at posterior extremity of body. Parasitic in stomach (occasionally intestine) of marine teleosts.

TYPE-SPECIES. *Theletrum fustiforme* Linton, 1910 [by original designation].

COMMENT. We agree with Yamaguti (1971) that this genus is monospecific. We do not agree, however, that the remainder of the species allocated to this genus should be placed in *Genolinea* Manter, 1925, and have, therefore, erected a new genus, *Neotheletrum*, in the Opisthadeninae to

accommodate them (see p. 68). Our observations of the type-species confirm that a uterine seminal receptacle is present as indicated by Yamaguti's (1971) and possibly Vigueras' (1958) figures. *Bunocotyle sudatlantica* Parukhin, 1976, may belong to this genus, as it possesses many morphological similarities and is recorded from the same family of host (Chaetodontidae). Parukhin's (1976a) description, however, indicates that there is a single vitelline mass and a cyclocoel present. Nevertheless, when viewed from certain angles *T. fustiforme* can appear to possess only one vitelline mass, and the presence or absence of a cyclocoel is often difficult to ascertain in this family. Certainly, Parukhin's material does not fit within our concept of *Bunocotyle*.

(?) *INDODEROGENES* Srivastava, 1937

Transverse ridge around body posterior to ventral sucker apparently absent. Gut-caeca terminate close to anterior margin of ovary. Testes separated by uterine coils. Seminal vesicle saccular (flask-shaped). Pars prostatica tubular. Sinus-sac (?) absent. Hermaphroditic duct short. Sinus-organ small (? temporary). Genital atrium small. Ovary close to posterior extremity. Laurer's canal reported present (?). Uterine coils entirely or almost entirely in hindbody; entirely or almost entirely pre-ovarian. Vitellarium two tandem to oblique masses; posterior or postero-lateral to ovary; at posterior extremity of body. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Indoderogenes purii* Srivastava, 1937 [by monotypy].

COMMENT. This genus, initially defined in an abstract by Srivastava (1937b) and later (1941) des-cribed in more detail, is known from only three specimens. In gross morphology it appears similar to the other two genera of this subfamily, although Srivastava (1941) reported the presence of Laurer's canal. We have some doubts about this, as such an observation on whole-mounts with a large, dense uterine field, as his figure indicates, must be questionable. Despite the fact that no mention was made by Srivastava of the presence of a sinus-sac, there may have been one present, as this structure is either small or weakly developed in the other genera of this subfamily.

If Laurer's canal is proved to be present by future workers, this genus should be transferred to the Halipeginae Poche, 1926, where, although sharing some of its features with *Deropegus* McCauley & Pratt, 1961, its gross morphology does not conform to the normal derogenid pattern. In addition, unlike the majority of halipegines this genus was recorded from a marine teleost, although the locality of the record, an almost land-locked bay in the Bay of Bengal, is brackish at certain times of the year.

MONOLECITHOTREMA Yamaguti, 1970   [T(w)]

Transverse ridges around body absent. Papillae may be present ventrally in forebody. Gut-caeca terminate blindly at posterior extremity. Testes close together, but sometimes separated by uterus. Seminal vesicle tubular; usually extending back dorsally to ventral sucker. Pars prostatica tubular; poorly developed; linked to seminal vesicle by aglandular duct. Sinus-sac small; poorly developed; may be slightly extruded through genital pore. Ovary well inside posterior half of hindbody. Small proportion of uterus may be coiled in forebody; small part of uterus extends posteriorly to vitellarium. Vitellarium one large, entire mass; immediately post-ovarian. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Monolecithotrema kala* Yamaguti, 1970 [by original designation].

COMMENT. Examination of 14 paratype-specimens mounted on a single slide shows that a uterine seminal receptacle is present, and that Yamaguti was probably mistaken in his observation of a small seminal receptacle between the ovary and the vitellarium. This structure corresponds with the position of Mehlis' gland, but might also have been part of the uterine seminal receptacle, Juel's organ (until sectioned material is examined we are assuming that this is present) or even a diverticulum of the gut-caeca. As in *Theletrum*, the uterine seminal receptacle tends to extend posteriorly to the vitellarium.

Family DEROGENIDAE Nicoll, 1910

Halipegidae Poche, 1926
Liocercidae Ejsmont, 1931

Body normally small; usually spindle-shaped to elongate oval. Ecsoma absent. Body-surface smooth. Oral and ventral suckers well developed; ventral sucker usually near middle of body, occasionally more anterior or posterior. Pharynx well developed. Oesophagus short. 'Drüsen-magen' usually present. Gut-caeca end blindly or form cyclocoel. Testes two; symmetrical to tandem; pre- or post-ovarian; in hindbody. Seminal vesicle thin-walled; oval, elongate or tubular; not constricted into portions; in forebody; occasionally partly or wholly enclosed within sinus-sac. Pars prostatica usually tubular, occasionally vesicular; occasionally enclosed within sinus-sac. Ejaculatory duct short or absent; often within sinus-sac. Sinus-sac normally present, occasion-ally absent; usually small and oval; often weakly developed; may enclose all or part of pars prostatica and seminal vesicle. Permanent sinus-organ present as small cone or absent. Herma-phroditic duct normally present; occasionally absent; usually short. Genital atrium present or absent; usually small. Genital pore mid-ventral in forebody. Ovary oval; pre- or post-testicular. Mehlis' gland normally post-ovarian or occasionally at level of ovary. Seminal storage and dis-posal apparatus variable. Laurer's canal usually present; either opening dorsally to exterior or leading into Juel's organ; often dilated proximally to form small rudimentary seminal receptacle, which is occasionally enlarged to form an apparently functional canalicular seminal receptacle. Juel's organ absent or present in either rudimentary or fully-developed state. Blind seminal receptacle present rarely. Uterine seminal receptacle normally present; rarely absent. Uterus may or may not extend posterior to vitellarium; significant proportion of uterus usually coiled in forebody. Eggs numerous; with or without filaments or threads; rarely with anopercular spine. Vitellarium one or two masses; entire or lobed (lobes normally shallow, rarely digitate); pre- or post-ovarian; symmetrical, oblique or tandem. Excretory vesicle Y-shaped; arms united in fore-body. Parasitic usually in gut (normally stomach) of freshwater and marine teleosts, but occasion-ally recorded from amphibians, reptiles and freshwater shrimps.

COMMENT. This is a family which does not have a constant seminal storage and disposal apparatus in the female system. As discussed below (p. 124), the variations of this apparatus probably occur because they are a diverse and successful, but relatively primitive group, which appear to have evolved at about the time when the first modifications of the primitive arrangement of the seminal storage and disposal apparatus began to occur. The variety of conditions found in this group tend to parallel those which have occurred during the evolution of some of the more advanced hemi-uroids, such as the hemiurids, bunocotylids and lecithasterids.

Key to Derogenidae

1. A. Testes posterior to ovary and vitellarium   .   .   .   .   .   **GONOCERCINAE** (p. 74)
   B. Testes anterior to ovary and vitellarium   2
2. A. Parasites primarily of freshwater teleosts, but occasionally present in brackish water or marine teleosts close to the ancient Sarmatic Sea region [Caspian, Black and Mediterra-nean Seas], in amphibians, in reptiles and in freshwater shrimps; ventral sucker occasionally anterior to middle of body; uterus not present posterior to vitellarium; sinus-sac, when present, may enclose part of or entire seminal vesicle and/or pars prostatica   .   .   .   .   **HALIPEGINAE** (p. 75)
   B. Parasitic in marine teleosts; ventral sucker not present in anterior half of body; uterus often extends posterior to vitellarium; sinus-sac present, never enclosing any part of pars prostatica or seminal vesicle .   .   .   .   **DEROGENINAE** (p. 71)

Subfamily DEROGENINAE Nicoll, 1910

(?) Liopyginae Ejsmont, 1931
(?) Liocercinae Ejsmont, 1931
Genarchinae Skrjabin & Guschanskaja, 1955
Orthoruberinae Nasir & Gomez, 1977

Ventral sucker in middle or posterior to middle of body. Gut-caeca end blindly or form cyclocoel. Testes pre-ovarian; symmetrical to oblique. Seminal vesicle small; globular to tubular. Pars prostatica usually tubular, occasionally vesicular; short or long. Sinus-sac present; globular to cylindrical. Permanent sinus-organ present; small; cone-shaped. Hermaphroditic duct normally short. Genital atrium small; often filled by sinus-organ. Ovary close behind testes. Laurer's canal present or absent; opening dorsally or into rudimentary Juel's organ; may be dilated proximally forming large rudimentary or functional canalicular seminal receptacle. Blind seminal receptacle present when Laurer's canal and uterine seminal receptacle absent; latter usually present. Uterus coiled throughout hindbody and part of forebody; significant proportion of uterus often present posterior to vitellarium. Eggs without filaments or threads, but may have anopercular spine. Vitellarium two symmetrical to tandem, oval or slightly indented masses; posterior or occasionally lateral and postero-lateral to ovary. Parasitic in gut (mainly stomach) of marine teleosts.

Key to Derogeninae

1. A. Uterus not normally extending posterior to vitellarium 4
   B. Significant proportion of uterus posterior to vitellarium 2
2. A. Cyclocoel present . . . . ***PROGONUS***
   B. Gut-caeca end blindly 3
3. A. Eggs drawn into sharp point at anopercular pole . . . . ***DEROGENOIDES***
   B. Eggs lacking point at anopercular pole . . . . ***DEROGENES***
4. A. Vitelline masses tandem to oblique, lateral and postero-lateral to ovary; blind seminal receptacle present . . . . ***LEURODERA***
   B. Vitelline masses symmetrical to oblique, post-ovarian; Laurer's canal and presumably uterine seminal receptacle present . . . . ***GONOCERCELLA***

COMMENT. Initially, we considered *Gonocercella* and *Leurodera* to be members of the Halipeginae because of the pre-vitelline distribution of the uterus. The fact that they parasitize marine teleosts and the structure of the terminal genitalia, however, clearly associated them with the Derogeninae. It could also be argued that *Arnola, Magnibursatus* and *Tyrrhenia*, which are present in teleosts from the brackish to marine conditions of the Black and Mediterranean Seas, should be included in the Derogeninae. The structure of the terminal genitalia, however, is different from that of the latter group. In addition, these three genera are morphologically related to some of the Asian halipegines from freshwater and can be historically and zoogeographically related to the hali-pegines of the central Asian region via the ancient Sarmatic Sea.

<div align="center">

DEROGENES Lühe, 1900   [n(w,s)]

</div>

(?) *Liopyge* Looss, 1899
(?) *Liocerca* Looss, 1902

Gut-caeca end blindly near posterior extremity. Testes symmetrical to oblique. Seminal vesicle globular to tubular and sinuous. Pars prostatica short to long. Sinus-sac globular. Male and female ducts unite within sinus-organ. Ovary usually close behind testes; may be lateral to posterior testis when latter is oblique. In *D. varicus* Laurer's canal opens distally into rudimentary Juel's organ and dilates proximally forming large rudimentary seminal receptacle. Uterine seminal receptacle present. Uterine field usually extends from posterior extremity to region of genital pore; significant proportion of uterus posterior to vitellarium. Eggs without anopercular spine. Vitelline masses symmetrical to oblique; globular or slightly indented; post-ovarian. Parasitic in stomach, oesophagus or occasionally gall-bladder of marine (? and freshwater) teleosts.

TYPE-SPECIES. *Derogenes ruber* Lühe, 1900 [by monotypy].

COMMENT. The overall morphology of *Liopyge bonnieri* (Monticelli, 1893) is probably identical to that of *Derogenes*, if the vitellarium and the testes have been confused. It is difficult to believe, however, that an experienced worker like Monticelli would make such a mistake, especially as he originally considered his specimens to be *Distoma varicum* [now *Derogenes varicus* (Müller, 1780)], and later re-named them *Distoma bonnieri*. Monticelli recorded this species from *Trigla*

gurnardus in the English Channel. Evidence against the validity of the genus *Liopyge* is that in spite of the abundance of this host it has never been found a second time, although *Derogenes varicus* has been recorded from the English Channel in *Trigla gurnardus* by Nicoll (1914) and in *T. lucerna* by Nicoll (1914), Baylis & Jones (1933) and by ourselves: we have re-checked the determination of the last two records. Until there is more conclusive evidence for the existence of *Liopyge*, therefore, we are including this genus, and its synonym *Liocerca*, as questionable synonyms of *Derogenes*.

The genus *Pronopyge* Looss, 1899, has been considered to be a close relative of *Liopyge* (see Yamaguti, 1971). Its type-species was originally quoted as *P. ocreata* (Rudolphi, 1802); but *Fasciola ocreata* of Rudolphi (1802) was shown by Odhner (1911) to be a species of *Hemiurus*, and, as stated by Poche (1926), *Pronopyge* must be considered a junior synonym of the latter genus. Monticelli (1891) considered *Distoma ventricosum* Rudolphi, 1819 (and van Beneden, 1871) [*nec D. ventricosum* (Pallas, 1774)], and *Distomum carolinae* Stossich, 1889, to be synonyms of *Fasciola ocreata* Rudolphi, 1802. Figures of these two species by van Beneden (1871) and Stossich (1889) and of '*Apoblema ocreata*' by Monticelli (1891) suggest that they belong to the fellodistomid genus *Pseudopentagramma* Yamaguti, 1971 (a junior synonym of *Pronoprynna* Poche, 1926 – see Bray & Gibson, in prep.) and they are similar to figures of *Pseudopentagramma symmetrica* (Chulkova, 1939) produced by Margolis & Ching (1965).

DEROGENOIDES Nicoll, 1913

Gut-caeca end blindly. Testes symmetrical to oblique. Seminal vesicle small; globular. Pars prostatica short. Sinus-sac somewhat cylindrical with proximal end slightly enlarged. Sinus-organ (?) presumably present. Ovary immediately posterior to testes. Laurer's canal and Juel's organ (?). Seminal receptacle (? rudimentary) reported. Uterine seminal receptacle (?). Much of uterus present posterior to vitellarium. Eggs drawn out to sharp point at anopercular pole. Vitelline masses entire; symmetrical; post-ovarian. Parasitic in stomach and intestine of marine teleosts.

TYPE-SPECIES. *Derogenoides ovacutus* Nicoll, 1913 [by original designation].

COMMENT. *Derogenoides skrjabini* Vlasenko, 1931, was made the type-species of *Magnibursatus* by Naidenova (1969). *D. tetralecithum* Roman, 1955, and possibly *D. sargi* Pogoreltseva, 1954, also appear to be halipegines.

GONOCERCELLA Manter, 1940

Ventral sucker in posterior half of body. Gut-caeca end blindly. Testes oblique. Seminal vesicle tubular; coiled. Pars prostatica vesicular. Sinus-sac small. Sinus-organ a muscular cone. Ovary immediately posterior to testes; close to posterior extremity. Laurer's canal opens dorsally (according to MacCallum, 1913). Blind or canalicular seminal receptacle absent. Uterine seminal receptacle presumably present. Juel's organ presumably absent. Uterus mainly coiled in forebody; not reaching posterior to vitellarium. Eggs without anopercular spine. Vitelline masses entire; symmetrical; post-ovarian; close to posterior extremity. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Gonocercella pacifica* Manter, 1940 [by original designation].

LEURODERA Linton, 1910   [n(w)]

Orthoruberus Nasir & Gomez, 1977

Body oval; stout. Gut-caeca end blindly near posterior extremity. Testes symmetrical; largely or partly extra-caecal. Seminal vesicle tubular; slightly sinuous. Pars prostatica short; with few to many external gland-cells; may be partly tubular and vesicular anteriorly. Sinus-sac oval. Sinus-organ small (well developed and conical in *Orthoruberus*). Ovary just posterior to testes; close to posterior extremity. Laurer's canal, Juel's organ and uterine seminal receptacle apparently absent.

Blind seminal receptacle present; large; antero-ventral, antero-lateral or antero-dorsal to ovary. Uterus anterior to vitellarium; much of it pre-testicular. Eggs without anopercular spine. Vitelline masses entire or slightly indented; tandem to oblique; lateral and postero-lateral to ovary. Parasitic in gut (mainly stomach) of marine teleosts (especially Pomadasyidae).

TYPE-SPECIES. *Leurodera decora* Linton, 1910 [by original designation].

COMMENT. *Leurodera ocyri* Travassos, Teixeira de Freitas & Bührnheim, 1965, and *L. inaequalis* Travassos, Teixeira de Freitas & Bührnheim, 1966, are not, in our opinion, specimens of *Leurodera*. The descriptions appear to resemble *Lecithophyllum* and *Aponurus*, and Overstreet (1973) considered these two species to be synonyms of *Aponurus pyriformis* (Linton, 1910).

PROGONUS Looss, 1899 [t(w,s)]

Genarches Looss, 1902

Cyclocoel present. Testes symmetrical. Seminal vesicle elongate, spindle-shaped, elongate oval or globular. Pars prostatica short; slightly vesicular. Sinus-sac small; globular. Ovary sinistral; halfway between testes and posterior extremity. Canalicular seminal receptacle present. Laurer's canal ends blindly after passing dorsally through cyclocoel. Rudimentary Juel's organ present as small dilations of Laurer's canal at distal extremity and especially at junction with seminal receptacle. Uterine seminal receptacle absent. Uterus extends posteriorly to vitellarium; fills most of hindbody and some of forebody. Eggs without anopercular spine. Vitelline masses entire; symmetrical; post-ovarian. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Progonus muelleri* (Levinsen, 1881) [by original designation].

COMMENT. In agreement with Poche (1926) and Bray (in press), *Progonus* Looss, 1899, cannot be considered a junior homonym of *Progona* Berg, 1882 (Recommendation of Article 36, International Rules of Zoological Nomenclature, 1926; Article 56(a), International Code of Zoological Nomenclature, 1961).

The apparent canalicular seminal receptacle present in this genus is essentially a type of blind seminal receptacle, especially as Laurer's canal does not open dorsally. The canalicular seminal receptacle (*sensu stricto*) is not found in the Hemiuroidea, except in the case of *Trifoliovarium*, and is normally associated with the use of Laurer's canal as a vagina during copulation (see Gibson & Bray, 1975).

Subfamily **GONOCERCINAE** Skrjabin & Guschanskaja, 1955

Hemiperinae Yamaguti, 1958

Ventral sucker posterior to middle of body. Gut-caeca end blindly. Testes post-ovarian; tandem to symmetrical; near posterior extremity. Seminal vesicle usually small; oval to tubular; in forebody. Pars prostatica tubular; short; linked to seminal vesicle by short, aglandular duct. Sinus-sac absent or poorly developed. Sinus-organ absent or present as small, blunt cone. Hermaphroditic duct absent or short. Genital atrium small or apparently absent. Ovary between testes and vitellarium. Laurer's canal present; opening dorsally; dilated proximally forming small rudimentary seminal receptacle. Juel's organ absent. Uterine seminal receptacle present. Uterus entirely pre-ovarian; most of coils usually in forebody. Eggs filamented or not. Vitellarium two entire or indented, oval masses; symmetrical; antero- to postero-lateral to ovary. Parasitic in stomach or branchial cavity of marine teleosts.

Key to Gonocercinae

1. A.   Eggs without filaments; sinus-sac and sinus-organ absent (but see comment on *Gonocerca*)
   GONOCERCA

   B.   Eggs filamented; sinus-sac weakly developed; sinus-organ present.   .   .   *HEMIPERA*

GONOCERCA Manter, 1925 [t(w,s)]

Ventral sucker in posterior half of body. Testes tandem to almost symmetrical; at posterior extremity of body. Seminal vesicle small; thin-walled; oval; close behind genital pore. Pars prostatica short; tubular. Sinus-sac and sinus-organ absent [see Comment]. Hermaphroditic duct absent (assuming that the small cavity into which male and female ducts open is the genital atrium). Genital atrium small or apparently absent. Ovary median. Uterus entirely pre-ovarian; largely in forebody. Eggs without filaments. Vitelline masses lateral or antero-lateral to ovary; entire to indented. Parasitic in stomach of marine teleosts (especially in mid-ocean).

TYPE-SPECIES. *Gonocerca phycidis* Manter, 1925 [by monotypy].

COMMENT. Manter (1934) described *G. phycidis* and *G. crassa* with a genital papilla present in both, and Laurer's canal absent in the latter. Our sectioned material of *G. phycidis* indicates that a sinus-organ is absent and that a well-developed Laurer's canal is present (see Gibson, 1976: figs 14b and 14c).

Since Manter's work there have also been conflicting opinions as to the presence of Laurer's canal in *G. crassa*, Yamaguti (1938*b*) stating it to be present and Rees (1953) absent. Both Rees (1953) and Brinkmann (1975) agree that a small but distinct genital atrium and genital papilla (sinus-organ) are present in *G. crassa*. If this is so, this species can hardly be considered to be congeneric with the other species of the genus. In view of the great morphological variability of *G. phycidis* and the morphological similarity with *Derogenes varicus*, with which *G. crassa* has been recorded, we consider that any change in its taxonomic status should await a complete redescription.

HEMIPERA Nicoll, 1913 [t(w,s)]

Hemiperina Manter, 1934

Ventral sucker in posterior half of body. Testes symmetrical to oblique at posterior extremity. Seminal vesicle oval to tubular. Pars prostatica tubular; short. Seminal vesicle and pars prostatica may apparently be enclosed by common, sub-globular, parenchymatous capsule. Sinus-sac weakly developed; with diffuse musculature; enclosing base of sinus-organ and proximal region of genital atrium. Sinus-organ a blunt cone. Male and female ducts may open separately on sinus-organ or form short hermaphroditic duct. Ovary median. Uterus entirely pre-ovarian; largely in forebody. Eggs filamented. Vitelline masses antero- to postero-lateral to ovary; entire or slightly indented. Parasitic in stomach or branchial cavity of marine teleosts.

TYPE-SPECIES. *Hemipera ovocaudata* Nicoll, 1913 [by original designation].

Subfamily HALIPEGINAE Poche, 1926

Arnolinae Yamaguti, 1958
Monovitellinae Ataev, 1970

Ventral sucker usually near middle of body, occasionally more anterior or posterior. Gut-caeca end blindly or form cyclocoel. Testes pre-ovarian; symmetrical to oblique or occasionally tandem to oblique. Seminal vesicle globular to tubular; sometimes entirely or partly internal. Pars prostatica tubular to vesicular; normally short; sometimes internal. Sinus-sac present or absent; usually weakly developed; may enclose pars prostatica and all or part of seminal vesicle. Sinus-organ present or absent; when present usually small, poorly developed and cone-shaped. Hermaphroditic duct usually short, occasionally long; rarely absent. Genital atrium small. Ovary usually close to posterior extremity. Laurer's canal present; with dorsal pore or short and leading into Juel's organ. Rudimentary seminal receptacle often present when Laurer's canal opens dorsally. Blind or canalicular seminal receptacle absent. Uterine seminal receptacle present. Uterus entirely or almost entirely anterior to vitellarium; coils extend into forebody, except in cases with ventral sucker inside anterior half of body. Eggs with or without filaments or threads.

Vitellarium one or two masses at posterior extremity of body; usually entire, but sometimes with indistinct or digitate lobes. Excretory bifurcation normally in hindbody, occasionally in forebody. Usually parasitic in gut (normally stomach) of freshwater teleosts; also recorded from brackish water and marine teleosts close to the ancient Sarmatic Sea region (Caspian, Black and Mediterranean Seas), amphibians, reptiles and freshwater shrimps (the majority of genera occur in Asia).

COMMENT. Certain genera of halipegines are closely related, differing basically in the apparent presence or absence of filaments or threads on the eggs or in the degree of union between the two vitelline masses. One such group comprises *Allotangiopsis*, *Chenia*, *Genarchopsis*, *Monovitella* and *Tangiopsis*, all of which occur in central, southern and south-east Asia. Another such group is *Arnola*, *Magnibursatus* and possibly *Anguillotrema* and *Tyrrhenia*, which, with the exception of *Anguillotrema* from central China, come from the Black or Mediterranean Seas.

There appear to be fundamental differences in the seminal disposal apparatus in the female reproductive system, as some genera possess Laurer's canal with a dorsal opening and others have a fully developed Juel's organ. The systematic significance of this must await further work, because the arrangement in most of the genera is as yet unknown.

Key to Halipeginae

1. A. Eggs with filaments or threads 2
   B. Eggs without filaments or threads 8
2. A. Cyclocoel present 3
   B. Gut-caeca end blindly 4
3. A. Cyclocoel and excretory bifurcation in forebody . . . . *ALLOTANGIOPSIS*
   B. Cyclocoel and excretory bifurcation in hindbody . . . . *GENARCHOPSIS*
4. A. Vitellarium a single mass . . . . *CHENIA*
   B. Vitellarium two similar masses 5
5. A. Vitelline masses entire; sinus-sac completely enclosing pars prostatica and seminal vesicle; ventral sucker in anterior half of body; uterine coils retained in hindbody
      MAGNIBURSATUS
   B. Vitelline masses usually lobed; ventral sucker near middle of body or more posterior; uterine coils extend into forebody 6
6. A. Vitelline masses lobed (usually with 4 and 5 small lobes) or occasionally entire . . 7
   B. Vitelline masses with about 8 digitate extensions . . . . . *THOMETREMA*
7. A. Sinus-sac encloses pars prostatica and entire seminal vesicle; vitelline masses lobed
      ANGUILLOTREMA
   B. Sinus-sac usually weakly developed or (?) absent, sometimes enclosing prostatica gland-cells, occasionally enclosing pars prostatica, rarely enclosing distal extremity of seminal vesicle; vitelline masses usually lobed, occasionally entire . . . *HALIPEGUS*
8. A. Cyclocoel present; ventral sucker near middle of body; uterine coils extend into forebody 10
   B. Gut-caeca end blindly 9
9. A. Ventral sucker in anterior half of body; uterine coils retained in hindbody . . . 11
   B. Ventral sucker near middle of body; uterine coils extend into forebody. . *TYRRHENIA*
10. A. Vitellarium a single mass . . . . *MONOVITELLA*
    B. Vitellarium two similar masses situated close together . . . . *TANGIOPSIS*
11. A. Sinus-sac encloses pars prostatica and seminal vesicle . . . . . *ARNOLA*
    B. Sinus-sac small, not enclosing pars prostatica and seminal vesicle. . . *DEROPEGUS*

HALIPEGUS Looss, 1899   [t(w); n(w,s)]

Genarchella Travassos, Artigas & Pereira, 1928
Vitellotrema Guberlet, 1928
Dollfuschella Vercammen-Grandjean, 1960
Progenarchopsis Fischthal, 1976
Paravitellotrema Watson, 1976

Ventral sucker near middle of body. Gut-caeca end blindly. Testes symmetrical to slightly oblique. Seminal vesicle saccular. Pars prostatica short; often reduced. Sinus-sac usually weakly

developed or (?) absent; often enclosing pars prostatica and, on some occasions, distal extremity of seminal vesicle. Temporary sinus-organ may be developed as conical papilla (may occasionally be permanent); on some occasions male and female ducts open separately through this papilla. Hermaphroditic duct, when present, short. Genital atrium normally small. Ovary usually separated from testes by uterus, but not always. Laurer's canal present, with dorsal pore; proximal region dilate forming rudimentary seminal receptacle. Juel's organ absent. Uterus not extending posteriorly to vitellarium; usually with about equal distribution in fore- and hindbodies. Eggs with long, single filament at anopercular pole. Vitellarium two relatively symmetrical masses; usually clearly four- and five-lobed, sometimes indistinctly lobed or entire. Parasitic in upper regions of gut (usually stomach) of freshwater teleosts, amphibians and reptiles; those from amphibians often recorded from mouth, one record from ear (Cosmopolitan).

TYPE-SPECIES. *Halipegus ovocaudatus* (Vulpian, 1859) [by monotypy].

COMMENT. Our concept of *Halipegus* may be considered wide; but, until more of the constituent species have been carefully and critically described, we believe that this concept is the most useful. In particular there appears to be a need for careful descriptions of the terminal genitalia in this genus: that of the type-species, for instance, is poorly known. The vitellarium is rather variable, the paired masses being distinctly lobed in the type-species and in most other species in the genus, weakly or indistinctly lobed in some species [e.g. *H. kessleri* (Grebnitzky, 1872)] and entire in some species [e.g. *H.* [=*Vitellotrema*] *fusipora* (Guberlet, 1928), *H.* [=*Genarchella*] *parva* (Travassos, Artigas & Pereira, 1928) and the two species of *Paravitellotrema* Watson, 1976]. *Halipegus cryptorchis* Mañe-Garzon & Gascon, 1973, is morphologically similar to *Deropegus*, especially in the rather anterior position of the ventral sucker. It differs, however, in the eggs being filamented and that part of the uterus is coiled in the forebody.

ALLOTANGIOPSIS Yamaguti, 1971

Ventral sucker in middle of body. Cyclocoel present in forebody. Testes symmetrical to oblique. Seminal vesicle tubular, stout, recurved. Pars prostatica short, tubular; not delimited. Sinus-sac forms muscular wall surrounding hermaphroditic duct (?). Sinus-organ absent (?). Laurer's canal and Juel's organ (?). Seminal receptacle reported [presumably either rudimentary type or Juel's organ]. Uterine seminal receptacle situated, at least partly, in distal region of uterus. Uterus not reaching posterior to vitellarium; significant proportion present in forebody. Eggs filamented. Vitellarium two lobed masses; slightly oblique; at posterior extremity. Excretory bifurcation in forebody. Parasitic in gonads of freshwater shrimps as (?) progenetic metacercaria (China).

TYPE-SPECIES. *Allotangiopsis shanghaiensis* (Yeh & Wu, 1955) [by original designation].

COMMENT. This genus is similar to *Tangiopsis*, differing only in the presence of filamented eggs and in the anterior positions of the cyclocoel and the excretory bifurcation. The latter differences might be explained by the relatively caudal position of the ventral sucker, a characteristic of metacercariae.

ANGUILLOTREMA Chin & Ku, 1974

Ventral sucker in posterior half of body. Gut-caeca end blindly. Testes symmetrical. Seminal vesicle tubular; coiled; internal. Pars prostatica vesicular; internal. Sinus-sac large; weakly muscled; enclosing pars prostatica and seminal vesicle. Sinus-organ muscular; conical. Laurer's canal and Juel's organ (?). Uterus entirely anterior to vitellarium; large proportion in forebody. Eggs with a filament at each end and small threads surrounding base of filament at one end. Vitellarium two masses with four and five lobes; symmetrical at posterior extremity. Parasitic in stomach of eels in freshwater (China).

TYPE-SPECIES. *Anguillotrema papillatum* Chin & Ku, 1974 [by original designation].

ARNOLA Strand, 1942 [t(w,s)]

Arnoldia Vlasenko, 1931, *nec* Mayer-Eymar, 1887

Ventral sucker in anterior half of body. Gut-caeca end blindly close to posterior extremity. Testes oblique; separated by uterus. Seminal vesicle coiled, tubular; internal. Pars prostatica short, straight; internal. Sinus-sac enclosing seminal vesicle and pars prostatica plus metraterm distally. Permanent sinus-organ absent. Short hermaphroditic duct and genital atrium present. Ovary immediately posterior to hind testis. Short, dilate Laurer's canal, containing sperm, opens into well-developed Juel's organ. Uterine seminal receptacle present. Uterus entirely anterior to vitellarium; coils not extending into forebody. Eggs without filaments. Vitellarium two symmetrical masses; situated close together at posterior extremity; slightly indented, usually indicating three and four lobes. Parasitic in stomach of marine teleosts (*Diplodus*) in Black Sea and Adriatic Sea.

TYPE-SPECIES. *Arnola microcirrus* (Vlasenko, 1931) [by original designation].

COMMENT. The low salinity of the Black Sea and the similarity between this genus and several genera from freshwater in Central Asia and the Far East suggest that *Arnola* might be a relict from the ancient Sarmatic Sea, which arose in the upper Miocene epoch, contained brackish water and extended from the Black Sea region easterly into Central Asia. Our finding *Arnola* in the Adriatic Sea in no way invalidates this hypothesis, as a connection between this region of the Mediterranean Sea and the Sarmatic Sea (then called the Karangat Sea) occurred briefly during the Pleistocene epoch [see Zenkevitch, 1947; Ekman, 1953; Miller, 1972].

This genus appears to be closely related to *Magnibursatus*, *Anguillotrema* and *Tyrrhenia*.

CHENIA Hsu, 1954

Ventral sucker just posterior to middle of body. Gut-caeca terminate blindly at level of ovary. Testes oblique. Seminal vesicle a curved, elongate sac. Pars prostatica internal (?; see figure 1 of Hsu). Sinus-sac enclosing attenuated anterior portion of seminal vesicle and pars prostatica. Sinus-organ not reported. (?) Seminal receptacle (presumably either rudimentary or Juel's organ) reported. Uterus entirely pre-ovarian; coils extending into forebody. Eggs reniform; with two filaments at one pole. Vitellarium single compact mass at posterior extremity. Parasitic in gut of freshwater gobiid teleosts (China).

TYPE-SPECIES. *Chenia cheni* Hsu, 1954 [by monotypy].

DEROPEGUS McCauley & Pratt, 1961

Parahalipegus Wootton & Powell, 1964

Ventral sucker in anterior half of body. Gut-caeca end blindly near posterior extremity. Testes tandem, oblique or symmetrical. Seminal vesicle saccular. Pars prostatica short; tubular to slightly vesicular; surrounded by dense layer of gland-cells. Sinus-sac apparently present, but weakly developed; small. Sinus-organ a muscular cone. Ovary usually separated from testes by loops of uterus. Laurer's canal present; apparently opening dorsally; slightly dilated proximally, forming a rudimentary seminal receptacle. Juel's organ presumably absent. Uterine coils not extending into forebody; one loop may reach posterior to vitellarium. Eggs without filaments. Vitellarium two symmetrical to oblique, entire or slightly lobed masses; close to posterior extremity. Parasitic in stomach of amphibians and teleosts in freshwater (North America).

TYPE-SPECIES. *Deropegus aspina* (Ingles, 1936) [by original designation].

GENARCHOPSIS Ozaki, 1925

Ophiocorchis Srivastava, 1933
(?) *Pseudogenarchopsis* Yamaguti, 1971

Ventral sucker in posterior half, or occasionally in middle, of body. Cyclocoel present in hind-body; oesophageal pouch often present. Testes usually oblique, occasionally symmetrical. Seminal vesicle tubular to elongate-saccular; coiled. Pars prostatica short; may be slightly vesicular. Sinus-sac not clearly described, but may be weakly developed and enclose pars prostatica and perhaps distal extremity of seminal vesicle. Sinus-organ a strongly muscular, blunt cone. Ovary usually sinistral and well posterior to testes. Laurer's canal opening into well-developed Juel's organ, or apparently opening dorsally (?). Uterus entirely pre-ovarian; coils extending into forebody. Eggs with long, polar filament. Vitellarium two entire or indented masses at posterior extremity; symmetrical to oblique. Parasitic mainly in stomach of freshwater teleosts, but there are two records from amphibians and two probable accidental infestations of snakes (Southern Asia and Far East).

TYPE-SPECIES. *Genarchopsis goppo* Ozaki, 1925 [by original designation].

COMMENT. *Genarchopsis thapari* Gupta & Chakrabarti, 1967, from the intestine of a snake, is known only from four immature worms, and it is probably a fish-parasite which has been in-gested by the wrong host. Yamaguti (1971) erected the genus *Pseudogenarchopsis* for this species; but his only apparent valid criterion for doing so is that this species is purported to have a cirrus-sac. As far as *Ophiocorchis* is concerned, this genus is said to differ from *Genarchopsis* in possessing an oesophageal pouch. Rai (1972) found this feature either present or absent in one species (*G. goppo*), and it cannot be considered a character of generic importance.

A well-developed Juel's organ in *G. punctati* Agrawal, 1966, was described by Anjaneyulu (1967) and Madhavi & Rao (1974); but Ozaki (1925) described *G. goppo*, the type-species, as having Laurer's canal which opened dorsally. It seems unlikely that species with such apparently different seminal and vitelline disposal apparatus could be congeneric, but more detailed information is required on *G. goppo* and other species in this genus in order to resolve this problem. Both Rai (1972) and Pandey (1975) also note the presence of Laurer's canal in *G. goppo*, but neither of them states how it terminates.

MAGNIBURSATUS Naidenova, 1969

Ventral sucker in anterior half of body. Gut-caeca end blindly close to posterior extremity. Testes oblique, in anterior hindbody. Seminal vesicle coiled, tubular; internal. Pars prostatica short, straight; internal. Sinus-sac enclosing seminal vesicle and pars prostatica, plus the metraterm distally; in forebody. Sinus-organ absent. Short hermaphroditic duct or genital atrium present. Laurer's canal ends blindly (? in Juel's organ). Uterine seminal receptacle present. Ovary near posterior extremity; separated from testes by uterus. Uterus entirely anterior to vitellarium; coils not extending into forebody. Eggs with several (? six to eight) filaments (? threads) at each end. Vitellarium two oblique to symmetrical masses; close together at posterior extremity. Parasitic in stomach of euryhaline or marine teleosts (Black Sea region).

TYPE-SPECIES. *Magnibursatus skrjabini* (Vlasenko, 1931) [by original designation].

MONOVITELLA Ataev, 1970

Ventral sucker in middle of body. Cyclocoel present in hindbody. Testes symmetrical. Seminal vesicle saccular. Pars prostatica short; vesicular. Sinus-sac reported absent (figure suggests it might be present as weakly muscled, tubular jacket of hermaphroditic duct). Sinus-organ absent (?). Genital atrium short. Ovary lateral; apparently extra-caecal; situated between right testis and vitellarium. Laurer's canal and Juel's organ (?). Uterus almost entirely anterior to vitellarium, but descending loop reaches close to posterior extremity; coils extend into forebody. Eggs not filamented. Vitellarium a single, entire mass; lateral; apparently extra-caecal between ovary and posterior extremity. Parasitic in intestine of brackish water teleosts (Caspian Sea).

TYPE-SPECIES. *Monovitella cyclointestina* Ataev, 1970 [by original designation].

COMMENT. *Monovitella*, despite certain apparent differences, is remarkably similar to *Tangiopsis*,

both of which are reported from gobiid fishes. Future work might show the two to be synonymous. *Chenia* is also morphologically similar and reported from gobiid fishes.

TANGIOPSIS Skrjabin & Guschanskaja, 1955

Ventral sucker in middle of body. Cyclocoel present; caeca unite anterior to testes. Testes symmetrical to oblique. Seminal vesicle tubular; recurved. Pars prostatica small; free in parenchyma (according to Tang, 1951; but his figure suggests that the prostatic glands may be delimited or that the duct is vesicular and he has omitted the external gland-cells). Sinus-sac apparently absent. Temporary sinus-organ may be present (?). Ovary between right testis and vitellarium. Laurer's canal opens dorsally. Juel's organ presumably absent. Rudimentary seminal receptacle apparently present. Uterus not passing posterior to vitellarium; almost entirely pre-ovarian; coils extend into forebody; apparently filled with spermatozoa throughout most of its length. Eggs without filaments. Vitellarium two slightly indented, symmetrical masses; close together at posterior extremity; united by short duct. Parasitic in stomach of freshwater teleosts (China).

TYPE-SPECIES. *Tangiopsis chinensis* (Tang, 1951) [by original designation].

COMMENT: This genus is similar to *Monovitella*.

THOMETREMA Amato, 1968

Ventral sucker in middle of body. Gut-caeca end blindly near posterior extremity. Testes oblique to symmetrical; separated by loops of uterus. Seminal vesicle tubular; stout; attenuated anteriorly; recurved. Pars prostatica with narrow lumen; surrounded by dense, oval mass of gland-cells. Sinus-sac not reported, but possibly present surrounding long hermaphroditic duct (see figures of Szidat, 1954). Sinus-organ present as small papilla in base of oval genital atrium (not reported by Amato, 1968). Ovary near posterior extremity; separated from testes by many loops of uterus; may have slightly irregular outline. Laurer's canal and Juel's organ (?). Uterus entirely pre-ovarian; coils extending into forebody. Eggs with one polar filament. Vitellarium two symmetrical masses of about eight short, digitate lobes, which are irregularly expanded distally. Parasitic in stomach of freshwater teleosts (*Plecostomus*), occasionally in estuarine conditions (South America).

TYPE-SPECIES. *Thometrema magnifica* (Szidat, 1954) n. comb. [syn. *T. portoalegrensis* Amato, 1968 – type by original designation].

COMMENT. This genus was erected for a new species, *T. portoalegrensis*, from *Plecostomus commersoni* in Brazil by Amato (1968). The species *Gonocercella magnifica* was described by Szidat (1954) from the same host in the estuary of the River Plate and from *Plecostomus plecostomus* in a neighbouring locality to Amato's record. Szidat's description is identical to that of Amato, with the exception that he described and figured the terminal genitalia in more detail and did not observe the filament on the egg. Considering that there is no evidence that Szidat teased out the eggs or sectioned his specimens, we have little hesitation in synonymizing the two species, as the presence of filamented eggs is often difficult to ascertain in whole-mounts.

*TYRRHENIA** Paggi & Orecchia, 1975

Ventral sucker near middle of body. Gut-caeca end blindly near posterior extremity. Testes oblique. Seminal vesicle saccular, but attenuated distally; internal. Pars prostatica (?) short, tubular (according to Paggi & Orecchia the prostatica cells empty into the hermaphroditic duct); internal. Sinus-sac enclosing entire seminal vesicle and pars prostatica, plus metraterm distally. Permanent sinus-organ absent. Hermaphroditic duct short. Genital atrium apparently absent (or small). Laurer's canal present, with rudimentary seminal receptacle. Juel's organ absent. Uterine

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* Paggi & Orecchia (1974) first used this name in an abstract, but without an accompanying description.

seminal receptacle present. Ovary immediately posterior to hind testis. Uterine coils reach posteriorly to vitellarium and extend into forebody. Eggs without filaments. Vitellarium two entire, symmetrical masses; situated close together immediately posterior to ovary and close to posterior extremity. Parasitic in stomach and on gills of marine teleosts (*Blennius*) in Mediterranean (Tyrrhenian) Sea.

TYPE-SPECIES. *Tyrrhenia blennii* Paggi & Orecchia, 1975 [by original designation].

CHELATREMA Gupta & Kumari, 1970, *gen. inq.*
Genus of uncertain position

This genus was erected in an abstract by Gupta & Kumari (1970) for a new species, *C. smythi* [type by monotypy], from the Indian freshwater fish *Chela baccala*. It is said to belong to the subfamily Arnolinae of the family Hemiuridae. The genus is unrecognizable from the brief definition given, and appears to have characters unusual, or unknown, in the Hemiuroidea.

Family **DICTYSARCIDAE** Skrjabin & Guschanskaja, 1955

Cylindrorchiidae Poche, 1926
Aerobiotrematidae Yamaguti, 1958
Pelorohelminthidae Fischthal & Kuntz, 1964
Albulatrematidae Yamaguti, 1965
Tetrasteridae Oshmarin, 1965
Dollfustravassosiidae Teixeira de Freitas & Kohn, 1967

Body usually large; oval; stout or flattened. Ecsoma absent. Body-surface smooth. Oral and ventral suckers well developed; ventral sucker in anterior half of body. Pharynx well developed. Oesophagus short. 'Drüsenmagen' normally present (?). Gut-caeca end blindly close to posterior extremity. Testes two; large; symmetrical; oval or elongate; pre-ovarian; just posterior to ventral sucker. Seminal vesicle tubular; in forebody. Pars prostatica tubular. Sinus-sac well developed, poorly developed or absent. Permanent sinus-organ absent (? or present as small papilla); temporary sinus-organ may form. Genital atrium small or absent. Hermaphroditic duct well developed or indistinguishable from genital atrium; sometimes appears to be continuation of metraterm with ejaculatory duct entering laterally. Ovary oval or with four (or five) short or elongate lobes; normally separated from testes by loops of uterus. Juel's organ* and uterine seminal receptacle present. Laurer's canal and blind or canalicular seminal receptacle absent. Uterus almost entirely retained in hindbody; mainly pre-ovarian or with many loops in post-ovarian field. Eggs without filaments; may link together and form chains. Vitellarium with six to eight (usually seven, arranged three and four) oval to digitiform lobes, or with two lateral acinous groups of follicles or two compact multilobulate masses; postero- to antero-lateral or posterior to ovary. Excretory arms united in forebody. Parasitic in swim-bladder of physostomatous teleosts in a marine environment.

COMMENT: The almost unique niche of these parasites in the swim-bladder of physostomatous teleosts is shared in the Hemiuroidea by the genus *Isoparorchis*. Although considered to be closely related to the members of the Dictysarcidae by many authors, the latter genus differs because it occurs in a freshwater teleost and possesses several primitive features, such as Laurer's canal, a tubular vitellarium and a well-developed, muscular sinus-organ.

Key to Dictysarcidae

1. A.	Uterus mainly pre-ovarian	. . . .	2
B.	Uterine field mainly post-ovarian	. . **CYLINDRORCHIINAE** *subfam. inq.* (p. 83)	

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* Observed in *Elongoparorchis* (see Madhavi & Rao, 1974) and *Dictysarca* (see Manter, 1947).

2. A. Ovary oval (entire or irregularly lobed); vitellarium two compact multilobulate masses or two acinous bunches of follicles; hermaphroditic duct indistinguishable from genital atrium   .   .   .   .   **DICTYSARCINAE** (p. 82)

   B. Ovary 4- (or 5-) lobed; vitellarium 6–8 (usually 7) digitiform to oval lobes; hermaphroditic duct distinguishable from genital atrium.   .   .   .   **ALBULATREMATINAE** (p. 82)

Subfamily **DICTYSARCINAE** Skrjabin & Guschanskaja, 1955

Body stout. Cuticular ridge may encircle mid-hindbody. Testes oval; entire or irregularly lobed. Sinus-sac and sinus-organ absent. Hermaphroditic duct indistinguishable from genital atrium; tubular; short. Ovary oval; entire or irregularly lobed; in posterior third of hindbody. Uterus mainly pre-ovarian, but some loops present in post-ovarian field. Vitellarium two compact multilobulate masses or two acinous bunches of follicles; antero- or postero-lateral to ovary. Usually parasitic in marine eels.

Key to Dictysarcinae

1. A. Cuticular ridge encircling mid-hindbody absent; ovary irregularly lobed; vitellarium in two, compact, multilobulate masses   .   .   .   .   *DICTYSARCA*

   B. Cuticular ridge encircling mid-hindbody present; ovary unlobed; vitellarium two groups of acinous follicles .   .   .   .   *AEROBIOTREMA*

DICTYSARCA Linton, 1910

No cuticular ridge present encircling mid-hindbody. Testes irregularly lobed. Seminal vesicle sinuous. Pars prostatica well developed. Hermaphroditic duct appears to be continuation of metraterm, with ejaculatory duct entering laterally. Ovary large; irregularly lobed. Vitellarium two compact, multilobulate masses; antero-lateral to ovary. Parasitic in moray eels (*Gymnothorax*) and sea-horses (*Hippocampus*).

TYPE-SPECIES. *Dictysarca virens* Linton, 1910 [by original designation].

AEROBIOTREMA Yamaguti, 1958

Cuticular ridge present encircling mid-hindbody. Testes entire. Seminal vesicle sigmoid. Pars prostatica straight. Ovary small; entire. Vitellarium two acinous bunches of follicles; one antero- and one postero-lateral to ovary. Excretory arms with numerous anastomosing side branches, mostly lying close to caeca. Parasitic in marine eels (*Muraenesox*).

TYPE-SPECIES. *Aerobiotrema muraenesocis* Yamaguti, 1958 [by original designation].

Subfamily **ALBULATREMATINAE** Yamaguti, 1965

Pelorohelminthinae Fischthal & Kuntz, 1964
Tetrasterinae Oshmarin, 1965

Body flattened to stout. Testes large; oval or elongate. Sinus-sac present; well or poorly developed. Hermaphroditic duct distinguishable from genital atrium. Ovary four (or five) distinct, oval or elongate lobes; in middle or posterior half of hindbody. Uterus mainly pre-ovarian or extending throughout hindbody. Vitellarium seven (occasionally six or eight) digitiform to oval lobes; immediately posterior or postero-lateral to ovary. Parasitic in marine (? or brackish water) teleosts.

Key to Albulatrematinae

1. A. Vitelline lobes, ovarian lobes and testes oval; ovary in middle of hindbody; significant proportion of uterus post-ovarian.   .   .   .   .   *ALBULATREMA*

B. Vitelline lobes and ovarian lobes digitiform; testes elongate; ovary well inside posterior half of hindbody; most of uterus pre-ovarian . . . . . *ELONGOPARORCHIS*

ALBULATREMA Yamaguti, 1965

Body stout. Testes oval. Seminal vesicle tubular; narrow; convoluted [according to Yamaguti, 1965, the seminal vesicle is replaced by a vas deferens, the distal portion of which is strongly muscular, convoluted and enclosed by an apparently muscular capsule]. Pars prostatica sigmoid; delimited. Sinus-sac well developed; bulbous. Temporary sinus-organ may be present. Genital atrium absent or (?) small. Ovary in middle of hindbody; ovarian lobes oval. Uterus extends throughout hindbody, much of it post-ovarian. Vitelline lobes oval to pyriform. Parasitic in marine (? or brackish water) teleosts (*Albula*).

TYPE-SPECIES. *Albulatrema ovale* Yamaguti, 1965 [by original designation].

ELONGOPARORCHIS Rao, 1961   [n(w)]

Pelorohelmins Fischthal & Kuntz, 1964
Tetraster Oshmarin, 1965
Dollfustravassosius Teixeira de Freitas & Kohn, 1967

Body flattened to stout. Testes elongate. Seminal vesicle sinuous; may reach dorsally to ventral sucker. Pars prostatica short. Sinus-sac poorly developed; present only distally as vestige surrounding base of genital atrium. Sinus-organ a small papilla-like structure (? temporary). Hermaphroditic duct relatively long; formed as continuation of metraterm, with ejaculatory duct entering laterally. Genital atrium oval or elongate-oval. Ovary well inside posterior half of hindbody; ovarian lobes digitiform. Uterus mainly pre-ovarian. Eggs may be linked together forming chains. Vitelline lobes digitiform; with condensed follicular appearance. Parasitic especially in catfishes, such as *Arius*.

TYPE-SPECIES. *Elongoparorchis pneumatis* Rao, 1961 [by original designation].

COMMENT. In some descriptions of species of this genus Mehlis' gland has been considered to be the ovary and the ovary to be anterior lobes of the vitellarium (see Fischthal & Kuntz, 1964a; Teixeira de Freitas & Kohn, 1967; Fischthal & Thomas, 1968; but cf. Yamaguti, 1971).

Subfamily CYLINDRORCHIINAE Poche, 1926, *status emend.* (*subfam. inq.*)

[Original description inadequate.] Body elongate-oval. Testes elongate. Terminal genitalia not known. Ovary small; oval; just inside posterior half of hindbody. Uterus convoluted posterior to ovary; straight anterior to ovary. Vitellarium two clusters of small follicles; antero-lateral to ovary. Parasitic in marine (? or brackish water) teleosts (*Tetrodon*).

CYLINDRORCHIS Southwell, 1913, *gen. inq.*

Defined as subfamily.

TYPE-SPECIES. *Cylindrorchis tenuicutis* Southwell, 1913 [by original designation].

COMMENT. We have included *Cylindrorchis* as a *genus inquirendus* because the original description of *C. tenuicutis* is inadequate. Southwell (1913) states: 'As only very few specimens of this parasite were obtained, it was found impossible to satisfactorily make out with *certainty*, the precise details of the reproductive system. I am therefore not certain that the following description is absolutely correct in every detail'. If Southwell had confused the uterus with the vitellarium, the vitellarium for the ovary and the ovary for Mehlis' gland or Juel's organ, then it is conceivable that he may have been dealing with immature specimens of *Elongoparorchis*.

Theoretically, the oldest family-group name available in this family is Cylindrorchiidae Poche, 1926; but, due to the questionable validity of *Cylindrorchis*, we feel that it would be inadvisable, at this stage, to use this genus as the type-genus of the family.

Family HEMIURIDAE Looss, 1899

Lecithochiriidae Lühe, 1901
Dinuridae Looss, 1907
Elytrophallidae Skrjabin & Guschanskaja, 1954

Body usually small, but elongate. Ecsoma present, occasionally reduced or vestigial. Body-surface smooth or with annular plications; the latter occasionally being serrate giving a scaley appearance. Presomatic pit or ventro-cervical groove occasionally present. Oral and ventral suckers well developed; usually close together. Pharynx well developed. Oesophagus usually short. 'Drüsenmagen' normally present. Gut-caeca terminate blindly; usually within ecsoma. Testes two; tandem, oblique or symmetrical; pre-ovarian; in hindbody. Seminal vesicle tubular, saccular or constricted into portions; muscular or thin-walled; in fore- or hindbody. Pars prostatica of variable length; usually tubular, but occasionally vesicular; may be linked to seminal vesicle by aglandular duct. Ejaculatory duct, if present, usually short. Sinus-sac usually well developed, occasionally reduced or absent. Prostatic or ejaculatory vesicle occasionally present within sinus-sac. Hermaphroditic duct usually enclosed within sinus-sac. Permanent sinus-organ and genital atrium well developed, small or absent; temporary sinus-organ may form from hermaphroditic duct in some cases. Genital pore mid-ventral at level of oral sucker or pharynx. Ovary oval; usually entire; post-testicular. Mehlis' gland post-ovarian. Laurer's canal and canalicular or blind seminal receptacle absent. Juel's organ and uterine seminal receptacle present. Uterus coiled mainly in pre- and/or post-ovarian region of hindbody; few or no coils present in forebody; initially descending into or towards ecsoma and then ascending towards forebody. Eggs numerous; small; embryonated; rarely with a polar filament. Vitellarium varies between forms with seven tubular branches (three on one side of body, four on other) and forms with two distinct, oval masses; mainly post-ovarian. Excretory vesicle Y-shaped; arms united in forebody or not. Parasitic mainly in gut, especially stomach, of marine teleosts, occasionally present in gut of freshwater teleosts and lung of sea-snakes.

Key to Hemiuridae

1. A. Ejaculatory (or prostatic) vesicle present within sinus-sac, occasionally partly external
   [this vesicle should not be confused with a pars prostatic which is also present] . . 2
   B. Ejaculatory (or prostatic) vesicle absent 4
2. A. Long, convoluted hermaphroditic duct and thin-walled permanent sinus-organ present;
   seminal vesicle bipartite, anterior part muscular; vitellarium 2 irregularly oval masses
   GLOMERICIRRINAE (p. 90)
   B. Hermaphroditic duct relatively straight; permanent sinus-organ absent; seminal vesicle
   tubular or saccular and partitioned, usually thin-walled; vitellarium 7 digitiform to oval
   lobes or with tendency to form 2 distinct, often lobed, lateral masses; ecsoma sometimes
   reduced or apparently absent 3
3. A. Eggs with polar filament; commonly parasitic under surface of liver
   HYPOHEPATICOLINAE (p. 91)
   B. Eggs without polar filaments; normally parasitic in gut . LECITHOCHIRIINAE (p. 91)
4. A. Sinus-sac absent or poorly developed, when present usually of 'open'-type; seminal vesicle
   entirely or mainly thin-walled, usually constricted into portions; ecsoma sometimes
   poorly developed. . . . . PLERURINAE (p. 95)
   B. Sinus-sac present, usually well developed, occasionally small 5
5. A. Vitellarium 2 symmetrical to slightly oblique, entire or lobed masses 6
   B. Vitellarium 7 distinct oval to tubular lobes 8
6. A. Seminal vesicle oval or bipartite, in fore- or hindbody; ecsoma well developed; parasitic
   in gut of marine teleosts 7
   B. Seminal vesicle tubular, extending well into hindbody; ecsoma reduced; parasitic in lung
   of sea-snakes . . . . PULMOVERMINAE (p. 98)
7. A. Body-surface smooth; seminal vesicle in forebody, oval, thick-walled; sinus-sac very small
   LETHADENINAE (p. 95)
   B. Body-surface with plications or 'scales'; seminal vesicle in hindbody, oval or bipartite,
   thin- or partly to entirely thick-walled . . . . . HEMIURINAE (p. 85)

8. A. Seminal vesicle with thick muscular wall, oval; permanent sinus-organ normally delicate
and amuscular .   .   .   . **ELYTROPHALLINAE** (p. 89)
 B. Seminal vesicle thin-walled and oval, tubular or constricted into portions; permanent
sinus-organ large and muscular, reduced to small papilla or apparently absent
DINURINAE (p. 86)

Subfamily HEMIURINAE Looss, 1899

Ecsoma well developed. Body-surface plicated or 'scaley' (i.e. with crenulate plications). Presomatic pit absent. Testes tandem to oblique. Seminal vesicle thin-walled, or partially or slightly muscular; bipartite or oval; in hindbody. Pars prostatica tubular; long; gland-cells occasionally delimited by membrane. Sinus-sac present; often tubular; not enclosing prostatic vesicle. Permanent sinus-organ absent, but hermaphroditic duct may be protruded to form temporary sinus-organ. Genital atrium usually small, but variable in length. Ovary oval. Vitellarium composed of two distinct oval masses, but these may show slight tendency toward lobation in three and four style. Excretory arms united in forebody. Parasitic in stomach of marine teleosts.

Key to Hemiurinae

1. A. Seminal vesicle bipartite .   .   .   . *HEMIURUS*
 B. Seminal vesicle oval   2
2. A. Plications on body-surface normal .   .   .   .   .   . *PARAHEMIURUS*
 B. Plications on body-surface crenulate, giving 'scaley' appearance .   . *ANAHEMIURUS*

HEMIURUS Rudolphi, 1809   [t(w,s); n(w, s)]

Apoblema Dujardin, 1845
Pronopyge Looss, 1899 (see p. 73).
Metahemiurus Skrjabin & Guschanskaja, 1954

Body-surface with normal plications. Seminal vesicle constricted into two portions (? occasionally three), one of which may have thick, muscular wall.

TYPE-SPECIES. *Hemiurus appendiculatus* (Rudolphi, 1802) [by subsequent designation: Stiles & Hassall, 1898].

COMMENT. Two subgeneric names have been erected: *Metahemiurus* Skrjabin & Guschanskaja, 1954, based upon sucker-ratios, the extent of the surface plications and the length of the ecsoma; and *Neohemiurus* Slusarski, 1958, based upon the presence of plications on the ecsoma. The former features are either variable or only of specific value, and the latter feature, plications on the ecsoma, is extremely doubtful (see p. 48) and requires confirmation. *Metahemiurus* has been used at the generic level by Brinkmann (1975).

ANAHEMIURUS Manter, 1947

Body-surface with 'scaley' appearance (i.e. with crenulate plications). Seminal vesicle oval; with relatively thick, muscular wall.

TYPE-SPECIES. *Anahemiurus microcercus* Manter, 1947 [by original designation].

PARAHEMIURUS Vaz & Pereira, 1930   [t(w)]

Body-surface with normal plications. Seminal vesicle oval; with muscular wall of variable thickness.

TYPE-SPECIES. *Parahemiurus merus* (Linton, 1910) [syn. *P. parahemiurus* Vaz & Pereira, 1930 – type by original designation].

Subfamily **DINURINAE** Looss, 1907

Stomachicolinae Yamaguti, 1958

Ecsoma well developed; occasionally large. Body surface plicated or smooth (apparently occasionally striated). Presomatic pit absent. Testes symmetrical to tandem; usually oblique. Seminal vesicle thin-walled; oval to tubular; may be constricted into two to four portions; in forebody, dorsal to ventral sucker or in hindbody. Pars prostatica tubular or vesicular; short or long; may be linked to seminal vesicle by aglandular duct. Sinus-sac present; small or large; usually oval; not enclosing a prostatic vesicle. Permanent sinus-organ large and muscular, reduced to small papilla or apparently absent. Genital atrium usually well developed; deep or shallow (often depending upon contraction). Ovary usually oval; occasionally reniform or lobed. Terminal portion of uterus may or may not form distinct vesicle just outside sinus-sac. Vitellarium normally seven tubular lobes; three on one side, four on the other. Excretory arms united or not united in forebody. Normally parasitic in stomach of marine teleosts.

Key to Dinurinae

1. A. Seminal vesicle usually (but not always) constricted into portions; permanent sinus-organ present, but occasionally reduced to small papilla (sectioning usually required); pars prostatica usually linked to seminal vesicle by distinct aglandular duct . . 2
   B. Seminal vesicle not constricted into portions; permanent sinus-organ usually apparently absent, but may be present as small papilla; pars prostatica not normally linked to seminal vesicle by distinct aglandular duct 7
2. A. Body-surface with plications 3
   B. Body-surface without plications 4
3. A. Pars prostatica long, may be sparsely surrounded by gland-cells; seminal vesicle trilocular . . . . ***DINURUS***
   B. Pars prostatica short, connected to seminal vesicle by long aglandular duct; seminal vesicle variable, tubular, saccular or divided into 2 or 3 sections . . ***ECTENURUS***
4. A. Glandular region of pars prostatica short; excretory arms unite in forebody; distal end of uterus often vesicular 5
   B. Glandular region of pars prostatica long; distal end of uterus not vesicular . . . 6
5. A. Aglandular region of pars prostatica long; seminal vesicle dorsal or postero-dorsal to ventral sucker; sinus-sac usually dilate proximally . . . . . ***ERILEPTURUS***
   B. Aglandular region of pars prostatica short; seminal vesicle in forebody; sinus-sac elongate oval . . . . ***ATHERIA***
6. A. Parasitic in stomach of marine teleosts; pars prostatica connected to seminal vesicle by short aglandular duct; excretory arms not united in forebody . . ***PARADINURUS***
   B. Parasitic in intestine of freshwater teleosts . . . . (?) ***PROSTERRHURUS***
7. A. Anterior part of hindbody greatly attenuated; pars prostatica in two parts separated by long aglandular duct . . . . ***MECODERUS***
   B. Anterior part of hindbody with normal configuration; pars prostatica undivided . . 8
8. A. Ecsoma large; seminal vesicle oval or elongate-oval 9
   B. Ecsoma normal; seminal vesicle tubular and sinuous . . . . ***TUBULOVESICULA***
9. A. Seminal vesicle in forebody . . . . ***ALLOSTOMACHICOLA***
   B. Seminal vesicle in hindbody . . . . ***STOMACHICOLA***

COMMENT. We considered separating this group into two, using the features in the first part of the key, because of the functional association between the presence of a permanent sinus-organ and a seminal vesicle constricted into sections by sphincter muscles (see p. 129). The two groups, however, appear to grade into one another.

DINURUS Looss, 1907   [n(w,s)]

Body-surface with plications. Seminal vesicle trilocular, or occasionally quadrilocular; in anterior hindbody or occasionally postero-dorsal to ventral sucker. Pars prostatica long; may be densely or sparsely invested by gland-cells; linked to seminal vesicle by aglandular duct. Sinus-sac and

permanent sinus-organ present; of variable size. Ovary oval. Excretory arms not united in forebody.

TYPE-SPECIES. *Dinurus tornatus* (Rudolphi, 1819) [by original designation].

ALLOSTOMACHICOLA Yamaguti, 1958

Ecsoma enormous. Body-surface smooth. Seminal vesicle elongate-oval; in forebody. Pars prostatica short; vesicular [? or long, tubular; see fig. 13b of Chauhan, 1954]; not connected to seminal vesicle by distinct aglandular duct. Sinus-sac present; small; oval. Permanent sinus-organ apparently absent. Ovary reniform; may be indistinctly lobed. Majority of uterus within ecsoma; normally fills more than half of ecsoma. Excretory arms (?) united in forebody.

TYPE-SPECIES. *Allostomachicola secundus* (Srivastava, 1937) [by original designation].

COMMENT. *Stomachicola lepturusi* Gupta & Gupta, 1976, appears to belong to this genus.

ATHERIA Hafeezullah, 1975

Body-surface smooth. Seminal vesicle saccular; in forebody. Pars prostatica short, tubular; connected to seminal vesicle by short, aglandular duct. Sinus-sac present; elongate-oval. Permanent sinus-organ present; (?) long, muscular. Ovary oval. Distal extremity of uterus vesicular. Excretory arms united in forebody.

TYPE-SPECIES. *Atheria zakiae* Hafeezullah, 1975 [by original designation].

COMMENT. This genus is apparently close to *Erilepturus* as a terminal dilation of the uterus occurs in both genera, although it has not been reported in all species of *Erilepturus*. The differences in the shape of the sinus-sac and in the length of the aglandular part of the pars prostatica are of questionable generic importance in this case; but we provisionally accept this genus on the basis of the distinct difference in the position of the seminal vesicle.

ECTENURUS Looss, 1907 [t(w); n(w)]

Magnacetabulum Yamaguti, 1934
Parectenurus Manter, 1947

Body-surface with plications. Seminal vesicle saccular, tubular or divided into two or three sections; postero-dorsal to ventral sucker or in anterior hindbody. Pars prostatica short (? or missing); connected to seminal vesicle by long, aglandular duct. Sinus-sac and permanent sinus-organ present; small. Ovary oval. Excretory arms not united in forebody.

TYPE-SPECIES. *Ectenurus lepidus* Looss, 1907 [by original designation].

ERILEPTURUS Woolcock, 1935 [n(w)]

Uterovesiculurus Skrjabin & Guschanskaja, 1954

Body-surface smooth (or finely transversely striated). Seminal vesicle variable; (?) oval, tubular to trilocular in the same species; dorsal or postero-dorsal to ventral sucker. Pars prostatica short, tubular; connected to seminal vesicle by long, aglandular duct. Sinus-sac present; dilate proximally (? or tubular). Permanent sinus-organ present; small. Ovary oval. Distal extremity of uterus (outside sinus-sac) may be vesicular. Excretory arms united in forebody.

TYPE-SPECIES. *Erilepturus tiegsi* Woolcock, 1935 [by original designation].

COMMENT. The vesicular nature of the terminal portion of the uterus, used by Skrjabin & Guschanskaja (1954) to erect *Uterovesiculurus*, is also found in *Erilepturus platycephali* (Yamaguti, 1934) according to Manter (1970), and possibly in other species of this genus. It is not clear whether this is a transient feature. In some species, such as those described by Yamaguti (1970), the proximal dilation of the sinus-sac is apparently missing.

MECODERUS Manter, 1940

Anterior part of hindbody attenuated. Body-surface smooth. Seminal vesicle saccular; well back in hindbody, just anterior to testes. Pars prostatica in two parts, one anterior to and other posterior to attenuated part of body, connected by long, aglandular duct; not connected to seminal vesicle by distinct aglandular duct. Sinus-sac present; small, oval. Permanent sinus-organ apparently absent. Ovary oval. Excretory arms united in forebody.

TYPE-SPECIES. *Mecoderus oligoplitis* Manter, 1940 [by original designation].

COMMENT. There are certain morphological similarities between this genus and *Stomachicola magna* (Manter, 1931).

PARADINURUS Vigueras, 1958 [t(w,s)]

Body-surface smooth. Seminal vesicle trilocular; at level of ventral sucker. Pars prostatica tubular; long; densely invested with gland-cells; connected to seminal vesicle by short, aglandular duct. Sinus-sac oval; thick-walled; relatively large. Permanent sinus-organ well developed. Ovary oval. Excretory arms not united in forebody.

TYPE-SPECIES. *Paradinurus manteri* Vigueras, 1958 [by original designation].

(?) *PROSTERRHURUS* Fischthal & Kuntz, 1963

Body-surface smooth. Seminal vesicle trilocular; in hindbody. Pars prostatica long, tubular; densely surrounded by gland-cells; apparently not linked to seminal vesicle by distinct, aglandular duct. Sinus-sac short; tubular. Permanent sinus-organ present; small. Ovary oval. Excretory arms (?). Parasitic in intestine of freshwater teleosts (? from estuarine region).

TYPE-SPECIES. *Prosterrhurus labeonis* Fischthal & Kuntz, 1963 [by monotypy].

COMMENT. The validity of this genus, which is based upon a single specimen, is questionable, because of shortcomings in its description and affinities with *Erilepturus*. The details of the terminal genital apparatus are based upon figure 687 of Yamaguti (1971). According to Fischthal & Kuntz (1963), there is an elongate sinus-sac which encloses the distal ends of the pars prostatica plus the metraterm, a prostatic vesicle, an ejaculatory duct and the hermaphroditic duct.

STOMACHICOLA Yamaguti, 1934

Pseudostomachicola Skrjabin & Guschanskaja, 1954
Acerointestinecola Jahan, 1970
Indostomachicola Gupta & Sharma, 1973

Ecsoma enormous. Body-surface smooth. Seminal vesicle oval; in hindbody. Pars prostatica tubular; long; sinuous; not connected to seminal vesicle by distinct aglandular duct; external gland-cells may not be evenly distributed throughout length. Sinus-sac present; small; oval. Permanent sinus-organ absent or reduced to rudiment. Ovary oval to reniform. Majority of uterine coils within ecsoma; normally fill less than half of ecsoma. Excretory arms united in forebody.

TYPE-SPECIES. *Stomachicola muraenesocis* Yamaguti, 1934 [by original designation].

TUBULOVESICULA Yamaguti, 1934 [n(s)]

Lecithurus Pigulewsky, 1938

Body-surface smooth. Seminal vesicle tubular; sinuous; in hindbody. Pars prostatica with long, wide lumen; sinuous or straight; not connected to seminal vesicle by distinct aglandular duct. Sinus-sac present; oval. Permanent sinus-organ normally absent, but may occur as small papilla.

Ovary oval to round. Vitelline lobes tubular, but often stout. Excretory arms united in forebody. Parasitic in stomach, body-cavity and body-tissues of marine teleosts (also reported from intestine of sea-snake).

TYPE-SPECIES. *Tubulovesicula spari* Yamaguti, 1934 [by original designation].

COMMENT. See Sinclair *et al.* (1972) and Stunkard (1973) concerning *Tubulovesicula* v. *Stomachicola*. Several authors, such as Sogandares-Bernal (1959), consider *T. lindbergi* (Layman, 1930) to be a senior synonym of the type-species of this genus.

Subfamily **ELYTROPHALLINAE** Skrjabin & Guschanskaja, 1954

Musculovesiculinae Skrjabin & Guschanskaja, 1954

Ecsoma well developed. Body-surface smooth or plicated. Pre-somatic pit absent, but ventro-cervical groove often present. Testes tandem to symmetrical, usually oblique. Seminal vesicle with exceptionally thick, muscular wall; oval, not constricted into portions; present in forebody, dorsal to ventral sucker or in hindbody. Pars prostatica tubular; long or short; usually linked to seminal vesicle by short, aglandular duct. Sinus-sac present; commonly tubular, long; not enclosing ejaculatory or prostatic vesicle. Sinus-organ usually well developed, but delicate and amuscular. Genital atrium usually deep (depending upon contraction). Ovary oval. Eggs rarely filamented. Vitellarium seven tubular to tear-shaped lobes, three on one side, four on the other, which may form rosette. Excretory arms united in forebody. Parasitic mainly in stomach of marine teleosts.

Key to Elytrophallinae

1. A. Body-surface with plications   2
    B. Body-surface without plications   4
2. A. Glandular region of pars prostatica mainly in hindbody   3
    B. Glandular region of pars prostatica in forebody   .   .   .   .   . *CLUPENURUS*
3. A. Sinus-sac long and narrow, reaching to the level of the seminal vesicle; vitelline lobes
            tear-shaped.   .   .   .   . *ELYTROPHALLOIDES*
    B. Sinus-sac relatively long, but not reaching to level of seminal vesicle; vitelline lobes
            tubular   .   .   .   . *LECITHOCLADIUM*
4. A. Seminal vesicle in forebody; eggs may be filamented .   .   . *MUSCULOVESICULA*
    B. Seminal vesicle in hindbody; eggs not filamented   .   .   . *ELYTROPHALLUS**

ELYTROPHALLUS Manter, 1940

Body-surface smooth. Seminal vesicle small to large; in hindbody. Pars prostatica sinuous; mainly or entirely in hindbody. Sinus-sac long, tubular, thick-walled. Vitelline lobes tear-shaped to digitiform. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Elytrophallus mexicanus* Manter, 1940 [by original designation].

(?) *CLUPENURUS* Srivastava, 1935

Body-surface with plications. Testes symmetrical to oblique. Seminal vesicle compact, oval; in hindbody. Pars prostatica in forebody. Sinus-sac bulbous; small. Vitelline lobes tubular. Parasitic in stomach of migratory clupeid teleosts (in freshwater).

TYPE-SPECIES. *Clupenurus piscicola* Srivastava, 1935 [by original designation].

COMMENT. The taxonomy of the hemiurid parasites of *Hilsa* (=*Clupea*; =*Ilisha*) *ilisha* is confused, as the descriptions of the species recorded either contain questionable features or are totally

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* *Johniophyllum* is inadequately described, but keys to this position.

inadequate. In addition to *Clupenurus piscicola*, the following species of hemiurid have been recorded from this host:

Lecithocladium ilishae Mamaev, 1970, *nec* Bashirullah & D'Silva, 1973.
Lecithocladium ilishae Bashirullah & D'Silva, 1973, *nec* Mamaev, 1970.
Lecithocladium chauhani Hafeezullah, 1975.

Some of these descriptions indicate relationships with the elytrophallines and others with the dinurines; but the problem cannot be resolved until a comparative study of these forms, some of which are probably synonymous, is undertaken.

ELYTROPHALLOIDES Szidat, 1955   [T(w,s); t(w,s)]

Body-surface with plications. Seminal vesicle large, reaching back to level of testes. Pars prostatica sinuous; in hindbody. Sinus-sac long, normally reaching back to level of seminal vesicle. Vitelline lobes tear-shaped. Parasitic in stomach of marine teleosts (in southern hemisphere).

TYPE-SPECIES. *Elytrophalloides oatesi* (Leiper & Atkinson, 1914) [syn. *E. merluccii* Szidat, 1955 – type by original designation].

(?) *JOHNIOPHYLLUM* Skrjabin & Guschanskaja, 1954

[Inadequately described.] Body-surface smooth. Seminal vesicle small; in hindbody. Details of sinus-sac and pars prostatica not known. Vitelline lobes digitiform. Parasitic in intestine of marine teleosts.

TYPE-SPECIES. *Johniophyllum johnii* (Yamaguti, 1938) [by original designation].

LECITHOCLADIUM Lühe, 1901   [t(w); n(w,s)]

Body-surface with plications. Oral sucker often funnel-shaped. Pharynx elongate. Seminal vesicle large; in hindbody. Pars prostatica long and sinuous; mainly or entirely in hindbody. Sinus-sac tubular; narrow; not reaching level of seminal vesicle and usually entirely or mainly in forebody. Vitelline lobes long and tubular. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Lecithocladium excisum* (Rudolphi, 1819) [by original designation].

MUSCULOVESICULA Yamaguti, 1940

Body-surface smooth. Seminal vesicle elongate; in forebody or overlapping ventral sucker. Pars prostatica short and indistinct; in forebody. Sinus-sac elliptical to pyriform; short. Vitelline lobes digitiform. Eggs may be filamented. Parasitic in stomach of marine teleosts (eels).

TYPE-SPECIES. *Musculovesicula gymnothoracis* Yamaguti, 1940 [by original designation].

Subfamily GLOMERICIRRINAE Yamaguti, 1958

Ecsoma well developed. Body-surface plicated. Pre-somatic pit absent. Testes oblique to tandem. Seminal vesicle bipartite; both parts globular to spindle-shaped; anterior part muscular; in hindbody or dorsal to ventral sucker. Pars prostatica tubular; short; linked to seminal vesicle by aglandular duct. Claviform sinus-sac present; in fore- or reaching into hindbody; enclosing prostatic vesicle. Hermaphroditic duct convoluted. Sinus-organ present; amuscular; long; convoluted. Genital atrium well developed. Vitellarium two irregularly oval, symmetrical masses. Excretory arms united in forebody. Parasitic in stomach of marine teleosts.

GLOMERICIRRUS Yamaguti, 1937   [n(w,s)]

Defined as subfamily.

TYPE-SPECIES. *Glomericirrus amadai* Yamaguti, 1937 [by original designation].

COMMENT. The interpretation of the terminal genitalia, based on our own sectioned material, differs markedly from the early descriptions (Yamaguti, 1937, 1938b). The observations of Manter (1970) and Campbell & Munroe (1977) agree with our interpretation.

Subfamily **HYPOHEPATICOLINAE** Skrjabin & Guschanskaja, 1954

Body spindle-shaped. Ecsoma reduced; appears to be permanently withdrawn. Body-surface smooth. Presomatic pit absent. Gut-caeca end blindly. Testes symmetrical at level of middle or posterior margin of ventral sucker. Seminal vesicle anterior or antero-dorsal to ventral sucker; constricted into two portions; elongate saccular; may be sinuous. Pars prostatica short; slightly vesicular; may be linked to seminal vesicle by short, aglandular duct. Sinus-sac present; oval; enclosing prostatic vesicle, part of metraterm and hermaphroditic duct. Permanent sinus-organ absent. Genital atrium present. Ovary oval. Much of uterus post-ovarian. Eggs with long, polar filament. Vitellarium seven digitiform lobes (three on one side, four on the other), forming post-ovarian rosette. Excretory arms united in forebody. Parasitic under connective tissue membrane of liver and in gut of marine teleosts.

HYPOHEPATICOLA Yamaguti, 1934 [t(w)]

Defined as subfamily.

TYPE-SPECIES. *Hypohepaticola callionymi* Yamaguti, 1934 [by original designation].

COMMENT. This representative of a monospecific subfamily was originally found under the connective tissue membrane of the liver, a very unusual habitat: it has also been recorded by Yamaguti (1942) from the stomach of the type-host, *Callionymus valenciennesi*, and from the intestine of *Monacanthus cirrhifer*. Yamaguti states, 'The proper location of the worm may be the stomach of *C. valenciennesi* as is the case with one of the present examples, but in fact it occurs more frequently on the surface of the liver. *M. cirrhifer* may be an accidental host.' We have examined material from the liver of *M. cirrhifer* collected by Dr A. Ichihara from Sagami Bay, Japan, in 1966, and specimens were recorded from the liver of *Callionymus flagris* by Ichihara *et al.* (1963), so it appears that the liver is the normal site of this parasite.

In our conception of *Hypohepaticola*, we have interpreted Yamaguti's (1934) 'distal portion of the pars prostatica' as being a prostatic vesicle and his 'small receptaculum seminalis' as being Juel's organ. In our view this genus is morphologically similar to the Lecithochiriinae, differing fundamentally according to the original description, only in the apparent absence of an ecsoma and the presence of filamented eggs. These two features are probably associated with the peculiar site of this parasite, as the presence of an ecsoma would not be significantly advantageous under the surface-membrane of the liver, whilst the presence of filaments on the eggs may aid their evacuation from the tissues of the host.

When we examined specimens from *M. cirrhifer* we could with some difficulty distinguish a withdrawn ecsoma. There is no evidence that this small structure is ever extruded. This suggests that *Hypohepaticola* is closely related to the Lecithochiriinae, especially as there is a tendency for the reduction of the ecsoma to occur in the latter group. For the present, however, we have retained the subfamily Hypohepaticolinae, because of the unusual habitat and the filamented eggs.

Hypohepaticola andamanensis Gupta & Miglani, 1974, from 'a teleost marine fish' off India, appears, from the brief description given, to possess none of the definitive characters of this genus. Their later (1976) description suggests that it is a lecithasterid.

Subfamily **LECITHOCHIRIINAE** Lühe, 1901

Sterrhurinae Looss, 1907
Brachyphallinae Skrjabin & Guschanskaja, 1955
Trithelaminae Yeh, 1955
Tricotyledoniinae Skrjabin & Guschanskaja, 1957
Dissosaccinae Yamaguti, 1958

Ecsoma usually well developed, occasionally reduced. Body-surface usually smooth, but occasionally plicated or rugate. Muscular 'shoulder-pads' present or absent. Presomatic pit and ventro-cervical groove present or absent. Testes tandem to symmetrical, usually oblique. Seminal vesicle elongate; constricted into two portions, which are occasionally separated by a duct, or tubular and convoluted; in bipartite forms anterior half may have thicker wall; normally in forebody, but forms with halves separated by duct may extend into hindbody. Pars prostatica short; vesicular or tubular; may extend slightly into base of sinus-sac; linked to seminal vesicle by short, aglandular duct. Sinus-sac present; rarely of 'open'-type; enclosing distinct ejaculatory or prostatic vesicle and metraterm. Permanent sinus-organ absent. Genital atrium usually small or absent, occasionally well developed. Ovary oval. Uterus mainly pre-ovarian or roughly equally distributed in pre- and post-ovarian fields. Eggs without filaments. Vitellarium seven digitiform to oval lobes in lateral groups of three and four, or with tendency to become two distinct lateral masses which often exhibit three and four lobes. Excretory arms united in forebody. Normally parasitic in gut of marine teleosts.

COMMENT. It is important to distinguish a prostatic (or ejaculatory) vesicle from a vesicular pars prostatica, otherwise difficulties of distinguishing some lecithochiriine and plerurine species become apparent. A prostatic (or ejaculatory) vesicle occurs entirely or mostly within a sinus-sac and together with a typical (external) pars prostatica from which it can be differentiated. In some plerurine genera which possess a recognizable sinus-sac, e.g. *Synaptobothrium*, the pars prostatica extends into the base of the 'open' sinus-sac, but the region of the pars prostatica inside the sinus-sac is indistinguishable from the region outside.

One could possibly divide the Lecithochiriinae into two groups:
(1) those with a distinctly seven-lobed vitellarium; and (2) those with a vitellarium composed of two entire or indistinctly lobed masses. We feel that the two groups do grade into one another, as the lobation in some species of *Lecithochirium* is reduced, whilst three- and four-lobed vitelline masses can be seen in some specimens of *Brachyphallus*. Some caution, therefore, should be exercised when using the key presented below.

Key to Lecithochiriinae

1. A. Vitellarium 7 distinct oval to digitiform lobes 2
   B. Vitellarium 2 entire masses which may be indistinctly 3- and 4-lobed 6
2. A. Large, muscular 'shoulder-pads' present 3
   B. Large, muscular 'shoulder-pads' absent 4
3. A. Small accessory sucker present anterior to oral sucker . . . ***TRICOTYLEDONIA***
   B. No small accessory sucker . . . . . . ***CYATHOLECITHOCHIRIUM***
4. A. Small muscular pad present anterior to oral sucker . . . . ***CATARINATREMA***
   B. Pre-oral lobe only present anterior to oral sucker 5
5. A. Large, eversible genital atrium present . . . . ***PLICATRIUM***
   B. Normal small genital atrium present . . . . . . ***LECITHOCHIRIUM***
6. A. Seminal vesicle composed of two parts separated by narrow duct and reaches into hindbody 7
   B. Seminal vesicle in forebody, tubular or bipartite, parts not separated by a duct. . . 8
7. A. Body-surface plicated anteriorly . . . . . . ***PSEUDODINOSOMA***
   B. Body-surface smooth . . . . ***DISSOSACCUS***
8. A. Seminal vesicle bipartite; body-surface plicated; deep presomatic pit present
                                                BRACHYPHALLUS
   B. Seminal vesicle a wide, convoluted tube; body-surface smooth; presomatic pit absent; ecsoma reduced . . . . ***PROLECITHOCHIRIUM***

LECITHOCHIRIUM Lühe, 1901   [t(w,s); n(w,s)]

Sterrhurus Looss, 1907
Ceratotrema Jones, 1933
Jajonetta Jones, 1933
Separogermiductus Skrjabin & Guschanskaja, 1955

Magniscyphus Reid, Coil & Kuntz, 1965
Neohysterolecitha Ahmad, 1977

Ecsoma well or poorly developed. Body-surface smooth. Pre-oral lobe rarely with two lateral knobs. Presomatic pit and/or ventro-cervical groove often present. Seminal vesicle bipartite, tripartite or occasionally coiled; in forebody. Pars prostatica tubular, with wide lumen, to vesicular. Short, narrow extension of pars prostatica and/or ejaculatory duct may be present within sinus-sac. Ejaculatory (or prostatic) vesicle linked posteriorly to antero-dorsally with pars prostatica or ejaculatory duct. Temporary sinus-organ may form. Vitellarium two lateral masses; usually divided into three and four oval to digitiform lobes. Parasitic in gut (mainly stomach) of marine teleosts; also recorded from body-cavity, hepatic ducts and gills of marine teleosts and (?) gut of freshwater reptiles.

TYPE-SPECIES. *Lecithochirium rufoviride* (Rudolphi, 1819) [by original designation].

COMMENT. *Sterrhurus* is supposed to be distinguished from *Lecithochirium* by the absence of a presomatic pit (Lloyd, 1938; Manter & Pritchard, 1960a). The systematic significance of the presomatic pit has been discussed by Jones (1943) and Nasir & Diaz (1971). It appears to us that observations of this character have, in the past, not been careful enough. Many authors appear to have mistaken the ventro-cervical groove, which occurs commonly in this genus, for a presomatic pit, with the result that some descriptions must remain questionable. For example, Nahhas & Short (1965) described specimens of *Lecithochirium mesosaccum* Manter, 1947, from *Sciaenops ocellata* with a presomatic pit and from *Synodus foetans* without. If this character is to be taken as distinguishing these two genera, it would appear that specimens from *Sciaenops* are not representative of the same genus as those from *Synodus*. If we assume that Nahhas & Short mistook the ventro-cervical groove, a structure with a transitory nature, for a presomatic pit which is a permanent structure (see p. 49), then the specimens can be considered synonymous. We have examined the type-species of *Lecithochirium* and can confirm that a small [compared with that of *Brachyphallus* and *Synaptobothrium*] presomatic pit is present. This is visible in sections, but barely so in whole-mounts. We can also confirm that this structure is absent in *Lecithochirium musculus* (Looss, 1907), the type-species of *Sterrhurus*. Considering its small size in *L. rufoviride* and the questionable value of some of the information in the literature, we consider it to be inadvisable at present to distinguish these two genera on this feature, although future work, involving the examination of many species in *transverse sections*, might show that it is a valid taxonomic criterion.

Another feature used to distinguish *Lecithochirium* from *Sterrhurus* is the presence of a prostatic vesicle in the former and an ejaculatory vesicle in the latter (Crowcroft, 1946). The difference between these two types of vesicle is the presence of a lining of gland-cells in the case of the prostatic vesicle [we prefer to call the latter a glandular ejaculatory vesicle]. It appears, however, that these gland-cells can be lost, their concentration in one species varies and that they may in fact be present or absent in the same species (Manter & Pritchard, 1960a; Nasir & Diaz, 1971). This feature, therefore, appears to be of little value, except as an aid to specific identification. Contrary to the work of other authors, e.g. Jones (1943), in our sectioned material of *L. rufoviride* there are no gland-cells lining the ejaculatory vesicle; but, as in the case of *L. musculus*, the distal ends of some of the cells lining the pars prostatica do extend into the proximal extremity of the vesicle.

Separogermiductus was distinguished from *Lecithochirium* in having 'a bulbous ejaculatory vesicle, almost as large or even larger than the pharynx, lined with a refractive non-cellular wall, empty of cells or droplets, and into which the pars prostatica enters dorsally and anteriorly' (Manter & Pritchard, 1960a). We have had the opportunity of examining specimens of *Lecithochirium genypteri* Manter, 1954, which is considered by Manter & Pritchard (1960a) to be a species of *Separogermiductus*. The terminal genitalia are very much like those of our specimens of *L. rufoviride*. The ejaculatory vesicle is, perhaps, a little larger in *L. genypteri*, but the lining of the ejaculatory vesicle and the point of entry of the pars prostatica into this vesicle are very similar. In both cases the pars prostatica passes over the dorsal wall of the vesicle and enters

antero-dorsally. As Jones (1943) shows the point of entry in *L. rufoviride* to be almost directly dorsal, it seems certain that this character varies to some extent, and is not reliable as a generic character.

With regard to *Magniscyphus*, the 'cup- or bowl-shaped' forebody is merely a variation of the ventro-cervical groove, which is common in many species of *Lecithochirium* (according to our definition). Indeed, a similar condition can be seen in fig. 38 of Looss (1908), in which he figures *L. musculus*. The occurrence of so-called prostatic cells around the hermaphroditic duct requires histochemical confirmation, as this may have been a case of the misinterpretation of the small gland-cells which commonly occur within the sinus-sac of hemiuroids. If these cells are prostatic, then it is more likely that they are associated with the distal extremity of the pars prostatica, which occasionally extends into the base of the sinus-sac. We do not consider that the presence of these cells is sufficient reason to substantiate the existence of *Magniscyphus* as a distinct genus from *Sterrhurus*, and hence *Lecithochirium*. In their useful work on *Lecithochirium*, Nasir & Diaz (1971), in addition to including *Sterrhurus*, *Separogermiductus* and *Magniscyphus* as synonyms of *Lecithochirium*, also considered *Synaptobothrium* and *Plerurus* likewise. We believe that Nasir & Diaz (1971) went too far with their synonymies, and that *Synaptobothrium* and *Plerurus* are valid genera.

BRACHYPHALLUS Odhner, 1905   [t(w,s)]

Body-surface plicated; plications may be crenulate. Presomatic pit present; circular or oval; deep; glandular. Seminal vesicle bipartite; anterior part small, posterior part large; thin-walled; occurring mostly in forebody. Pars prostatica tubular. Temporary sinus-organ may be seen. Vitellarium two lateral masses; entire, irregularly lobed or indistinctly three- and four-lobed. Parasitic in gut (stomach) of marine and migratory teleosts.

TYPE-SPECIES. *Brachyphallus crenatus* (Rudolphi, 1802) [by original designation].

COMMENT. The terminal genitalia were described in detail by Lander (1904) and Slusarski (1958), and we agree that a glandular ejaculatory (prostatic) vesicle is present.

CATARINATREMA Teixeira de Freitas & Santos, 1971

May bear papillae on ecsoma. Presomatic pit present. Muscular pad present anterior to oral sucker. Seminal vesicle bipartite; in forebody. Pars prostatica tubular. Vitellarium two masses of three and four short, digitiform lobes. Parasitic in stomach and intestine of marine teleosts.

TYPE-SPECIES. *Catarinatrema verrucosum* Teixeira de Freitas & Santos, 1971 [by original designation].

CYATHOLECITHOCHIRIUM Yamaguti, 1970

Body-surface smooth. Muscular 'shoulder-pads' present. Pre-oral accessory sucker absent. Seminal vesicle bipartite; anterior part with thick wall; in forebody. Pars prostatica may be partly within sinus-sac. Vitellarium seven digitiform lobes in two groups of three and four. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Cyatholecithochirium gymnothoracis* Yamaguti, 1970 [by original designation].

DISSOSACCUS Manter, 1947

Ecsoma well developed. Body-surface smooth. Seminal vesicle in two parts separated by narrow duct; one part normally mainly anterior and other mainly posterior to ventral sucker. Pars prostatica (?) tubular. Vitellarium two slightly indented masses. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Dissosaccus laevis* (Linton, 1898) [by original designation].

PLICATRIUM Manter & Pritchard, 1960

Papillae may occur on body-surface. Presomatic pit absent. Seminal vesicle bipartite; in forebody. Pars prostatica tubular. Large, eversible genital atrium present; wrinkled or convoluted when everted. Vitellarium seven digitiform lobes. Parasitic in intestine of marine teleosts.

TYPE-SPECIES. *Plicatrium lycodontis* (Myers & Wolfgang, 1953) [by monotypy].

PROLECITHOCHIRIUM Yamaguti, 1970

Ecsoma reduced. Body-surface smooth. Presomatic pit absent. Seminal vesicle tubular; convoluted and widening posteriorly; in forebody. Pars prostatica tubular. Vitellarium two compact masses. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Prolecithochirium pterois* Yamaguti, 1970 [by original designation].

COMMENT. This genus has many of the characteristics of *Lecithochirium*; but apparently lacks lobation of the vitellarium.

PSEUDODINOSOMA Yamaguti, 1970

Ecsoma well developed. Body-surface with crenulate plications (? giving 'scaley' appearance). Presomatic pit absent. Seminal vesicle in two parts separated by narrow duct; one part (convoluted) anterior and other (claviform) posterior to ventral sucker. Pars prostatica tubular. Vitellarium two slightly indented masses. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Pseudodinosoma macrorchis* Yamaguti, 1970 [by original designation].

TRICOTYLEDONIA Fyfe, 1954 [n(w,s)]

Grassitrema Yeh, 1955

Body-surface smooth. Muscular 'shoulder-pads' present. Presomatic pit absent. Pre-oral accessory sucker present. Seminal vesicle bipartite; posterior part elongate; anterior to posterior margin of ventral sucker. Pars prostatica vesicular; partly enclosed by sinus-sac; leads into small, aglandular ejaculatory vesicle; connected to seminal vesicle by short, aglandular duct. Vitellarium seven digitiform lobes. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Tricotyledonia genypteri* Fyfe, 1954 [by original designation].

Subfamily LETHADENINAE Yamaguti, 1971

Ecsoma well developed. Body-surface smooth. Pre-somatic pit absent. Testes oblique. Seminal vesicle oval; thick-walled; in forebody. Pars prostatica vesicular; with muscular wall; external gland-cells absent or weakly developed; separated from seminal vesicle by aglandular duct and from sinus-sac by long ejaculatory duct. Sinus-sac small; not containing ejaculatory or prostatic vesicle. Sinus-organ (?) present (? temporary); small. Genital atrium short. Vitellarium two symmetrical, unlobed, oval masses. Excretory arms not united in forebody. Parasitic in stomach of marine teleosts.

LETHADENA Manter, 1947

Defined as subfamily.

TYPE-SPECIES. *Lethadena profunda* (Manter, 1934) [by original designation].

PLERURINAE subfam. nov.

Body small; spindle-shaped to cylindrical. Ecsoma reduced or well developed. Body-surface smooth, or occasionally with crenulate plications giving a scaley appearance. Presomatic pit

absent, except in *Synaptobothrium*. Prepharynx absent. Pharynx well developed. Oesophagus short. 'Drüsenmagen' present. Gut-caeca terminate blindly inside ecsoma. Testes pre-ovarian; symmetrical to tandem, usually oblique. Seminal vesicle elongate, saccular and constricted into two, three or four sections; thin-walled, although certain sections may have thicker walls; in forebody or partly in hindbody. Pars prostatica vesicular or tubular; may be partly enclosed by muscles of sinus-sac; commonly linked to seminal vesicle by aglandular duct. Sinus-sac apparently absent or poorly developed; when present usually of 'open'-type. Permanent sinus-organ absent. Ejaculatory (prostatic) vesicle absent. Hermaphroditic duct commonly vesicular proximally and tubular distally. Genital atrium usually deep, but may be shallow. Genital pore mid-ventral in forebody. Ovary entire or lobed. Laurer's canal absent. Canalicular and blind seminal receptacles absent. Juel's organ present. Uterine seminal receptacle present. Uterus convoluted; passing back from ovary into ecsoma and then forward into forebody. Vitellarium post-ovarian; composed of two, four- and three-lobed, masses; the lobes being small to digitiform. Excretory vesicle Y-shaped; arms united in forebody. Parasitic in stomach of marine teleosts.

COMMENT. It is important, in this group, to distinguish between a vesicular pars prostatica and an ejaculatory (prostatic) vesicle. An ejaculatory vesicle occurs in the Lecithochiriinae, lacks external prostatic cells, is normally entirely enclosed within a distinct sinus-sac, and is present together with a normal pars prostatica which occurs externally to, or occasionally partly within, the sinus-sac. The vesicular pars prostatica of the Plerurinae varies from being completely outside the sinus-sac, if it is present, to being only partly enclosed by the muscles of a weakly developed sinus-sac of the 'open'-type.

Key to Plerurinae

1.	A.	Seminal vesicle tripartite in forebody, anterior and middle sections with thick, muscular wall	***VOITREMA***
	B.	Seminal vesicle saccular to 4-lobed or tubular, thin-walled	2
2.	A.	Seminal vesicle in forebody	3
	B.	Seminal vesicle at least partly extended into hindbody	4
3.	A.	Presomatic pit absent; vitelline lobes digitiform	***PLERURUS***
	B.	Presomatic pit present; vitelline lobes short	***SYNAPTOBOTHRIUM***
4.	A.	Body-surface has 'scaley' appearance	***DINOSOMA***
	B.	Body-surface smooth	***ADINOSOMA***

PLERURUS Looss, 1907   [t(w,s)]

Paraplerurus Fischthal & Kuntz, 1963
Merlucciotrema Yamaguti, 1971

Ecsoma reduced or well developed. Body-surface smooth. Testes symmetrical to oblique. Seminal vesicle in forebody; elongate; saccular, two-, three- or four-lobed; often sigmoid; thin-walled. Pars prostatica vesicular; may be linked to seminal vesicle by short aglandular duct (some authors maintain that this is a tubular region of the pars prostatica). Sinus-sac apparently absent or poorly developed and of 'open'-type. Hermaphroditic duct tubular; deep; possibly eversible. Ovary oval to lobed. Vitelline lobes tubular to digitiform.

TYPE-SPECIES. *Plerurus digitatus* (Looss, 1899) [by original designation].

COMMENT. Yamaguti (1970) points out that Looss (1908) figures a large oval seminal receptacle in the type-species, and suggests that what Looss actually saw was a uterine seminal receptacle. We confirm that a uterine seminal receptacle does occur in this species. Juel's organ has been described in *P. longicaudatus* (Yamaguti, 1953) by Madhavi & Rao (1974) and we have observed it in the type-species.

    Owing to its close phylogenetic relationship (see Fig. 9) with the Lecithochiriinae, we wondered whether the vesicular modification of the ejaculatory duct in this group might be a prostatic vesicle rather than a vesicular pars prostatica. Our observations of the type-species of this genus indicate that the structure present is a vesicular pars prostatica (see definition; p. 48). This is

not really surprising, if our suggestions as to its possible function are correct, because in the absence of a sinus-sac, there is no functional requirement for a prostatic vesicle.

We have included *Merlucciotrema*, which Yamaguti (1971) based upon Manter's specimen of *Sterrhurus praeclarus* Manter, 1934, as a synonym of *Plerurus*, because it appears to differ only in the reduced nature of the ecsoma and in that the vitelline lobes appear to be separated by narrow vitelline ducts. The size of the ecsoma is a variable feature in many hemiurid genera, even when contraction is taken into account, and Manter's original illustration suggests some evidence that the ecsoma of this species might be invaginated further than he indicates.

ADINOSOMA Manter, 1947

Body-surface smooth. Testes oblique. Seminal vesicle large, saccular, bipartite; postero-dorsal to ventral sucker. Pars prostatica vesicular, but elongate; connected to seminal vesicle by long, aglandular duct. Sinus-sac apparently absent. Hermaphroditic duct long, with poorly developed hermaphroditic vesicle proximally. Ovary unlobed. Vitellarium two indented or lobed masses.

TYPE-SPECIES. *Adinosoma robustum* (Manter, 1934) [by original designation].

COMMENT. This genus includes *A. hawaiiense* (Yamaguti, 1970) n. comb., a species which was originally placed in the genus *Dinosoma*.

DINOSOMA Manter, 1934   [T(w,s); n(w,s)]

Body-surface with crenulate plications, giving 'scaley' appearance. Testes symmetrical to tandem. Seminal vesicle postero-dorsal to ventral sucker; saccular, bipartite or wide; sinuous. Pars prostatica vesicular; may be connected to seminal vesicle by long, aglandular duct. Sinus-sac apparently absent. Hermaphroditic duct long, narrow; with small vesicle proximally. Ovary oval. Vitellarium two indented or lobed masses.

TYPE-SPECIES *Dinosoma rubrum* Manter, 1934 [by original designation].

SYNAPTOBOTHRIUM von Linstow, 1904   [t(w,s)]

Body-surface smooth. Presomatic pit present; circular or oval; deep; glandular. Testes oblique. Seminal vesicle bipartite (? or tripartite); anterior part small, posterior part long; thin-walled; occurring mostly in forebody, but may extend dorsal to ventral sucker. Pars prostatica tubular with wide lumen; may extend into base of sinus-sac. Sinus-sac weakly developed; of 'open'-type. Ovary oval. Vitellarium two lateral masses with three and four short lobes. Eggs may be reniform.

TYPE-SPECIES. *Synaptobothrium caudiporum* (Rudolphi, 1819) [syn. *S. copulans* von Linstow, 1904 – type by monotypy].

COMMENT. The sinus-sac in this genus is weakly developed and of the 'open'-type, and an ejaculatory (prostatic) vesicle is absent. We have, therefore, included it in the Plerurinae. The wide pars prostatica may extend into the base of the 'open' sinus-sac. *Lecithochirium apharei* Yamaguti, 1970, probably belongs to this genus.

(?) *VOITREMA* Yamaguti, 1971

[Inadequately known.] Body-surface (?). Testes oblique. Seminal vesicle tripartite; in forebody; anterior and middle sections with thick, muscular wall. Pars prostatica vesicular; may be partly enclosed by muscles of (?) sinus-sac; attached to seminal vesicle by short (?) aglandular duct. Sinus-sac (?) weakly developed; with diffuse musculature; of 'open'-type. Genital atrium sac-like. Ovary elongate oval. Vitelline lobes digitiform.

TYPE-SPECIES. *Voitrema amplum* (Manter, 1961) [by original designation].

COMMENT. This is a questionable genus based upon one inadequately described specimen.

Subfamily **PULMOVERMINAE** Sandars, 1961

Ecsoma reduced. Body-surface smooth (? spines reported within suckers). Presomatic pit absent. Testes tandem to oblique. Seminal vesicle tubular; long; thick-walled; reaches to or almost to level of testes. Pars prostatica short; vesicular; partly enclosed by sinus-sac. Sinus-sac present; not enclosing ejaculatory or prostatic vesicle. Sinus-organ variable in length, (? temporary). Genital atrium small. Ovary occasionally divided into dorsal and ventral lobes. Vitellarium two lateral, closely aligned masses; normally with three and four lobes. Excretory arms united in forebody. Parasitic in lung of sea-snakes.

PULMOVERMIS Coil & Kuntz, 1960

Hydrophitrema Sandars, 1960
Laticaudatrema Telford, 1967

Defined as subfamily.

TYPE-SPECIES. *Pulmovermis cyanovitellosus* Coil & Kuntz, 1960 [by original designation].

Family **HIRUDINELLIDAE** Dollfus, 1932

Botulidae Guiart, 1938
Lamprirematidae Yamaguti, 1940
Mediolecithidae Oshmarin, 1968
[Includes: Profundiellinae Skrjabin, 1958]

Body large; stout or elongate; contractile. Ecsoma absent. Body-surface smooth; may be papillate in forebody or wrinkled. Oral and ventral suckers well developed; latter in anterior half of body. Pharynx well developed. Oesophagus usually short. 'Drüsenmagen' present. Gut-caeca terminate blindly or form uroproct; sometimes fuse subterminally forming cyclocoel; usually diverticulate. Testes two; in tandem, oblique or symmetrical; pre-ovarian; in hindbody. Seminal vesicle tubular; normally thin-walled, occasionally partly thick-walled; convoluted in forebody. Pars prostatica well developed; tubular; usually long. Ejaculatory duct long; muscular; surrounded by muscular 'cirrus-sac'; opens into genital atrium through well-developed conical to cylindrical 'cirrus'. Hermaphroditic duct, sinus-sac and sinus-organ absent. Genital atrium large; usually capable of being everted. Genital pore mid-ventral in forebody. Ovary oval; post-testicular; in middle or anterior half of hindbody. Laurer's canal and uterine seminal receptacle normally present. Juel's organ and blind or canalicular seminal receptacle absent. Uterus descending ventrally and ascending more dorsally; coiled mainly at level of vitellarium, but often extending more anteriorly into pre-ovarian region; mainly inter-caecal, occasionally reaching extra-caecally; metraterm opens into genital atrium directly or through a papilla-like organ situated immediately posterior to 'cirrus'. Eggs numerous; small; without filaments. Vitellarium composed of from two to numerous long, straight or convoluted, branched tubules; mainly post-ovarian; inter- or extra-caecal. Excretory vesicle Y-shaped; arms initially dorso-ventrally oriented, convoluted, united in forebody. Parasitic in stomach (occasionally on gills) of large, carnivorous, marine teleosts.

COMMENT. In our opinion this family contains three monotypic genera which cannot be distinguished at the subfamily level. It is possible that *Distoma gigas* Nardo, 1827, from the stomach of *Luvarus imperialis* is a fourth genus; but, as suggested by Gibson & Bray (1977), there is some evidence that this species may be a sclerodistomid (see p. 113).

Key to Hirudinellidae

1. A.   Body stout, elongate or keyhole-shaped; uroproct present; 'cirrus-sac' small, globular;
        seminal vesicle entirely thin-walled   2
   B.   Body slender, elongate; uroproct absent; 'cirrus-sac' large, elongate; distal part of seminal
        vesicle with muscular wall   .   .   .   .   *LAMPRITREMA*

2. A. Vitellarium in two lateral fields between levels of testes and mid-hindbody; uterus mainly
        inter-caecal, post-ovarian, at level of vitellarium   .   .   .   .   . *HIRUDINELLA*
   B. Vitellarium massed close to ventral surface, inter-caecal between ovary and posterior
        extremity; uterus reaching extra-caecally, mainly in anterior hindbody   .   . *BOTULUS*

HIRUDINELLA de Blainville, 1828   [t(w,s)]

Hirudinella Garcin, 1730 [Pre-Linnaean; see Gibson, 1976]
Uroproctinella Skrjabin & Guschanskaja, 1957

Body stout, elongate or keyhole-shaped. Body-surface often transversely wrinkled. Uroproct
present; gut-caeca may fuse sub-terminally in older specimens forming cyclocoel. Testes sym-
metrical to oblique; in anterior hindbody. Seminal vesicle thin-walled throughout its length.
'Cirrus-sac' relatively small; globular. 'Cirrus' cone-shaped to digitiform. Genital atrium capable
of being everted through genital pore. Ovary in anterior hindbody. Uterus mainly inter-caecal;
coils extending posteriorly from ovary to near posterior limit of vitellarium. Vitellarium in two
lateral fields between testes and middle of hindbody. Parasitic in stomach of large carnivorous,
marine teleosts (usually scombroids).

TYPE-SPECIES. *Hirudinella ventricosa* (Pallas, 1774) [syn. *H. clavata* (Menzies, 1791) – type by
monotypy].

COMMENT. As discussed by Gibson (1976), it is likely that this genus is monotypic.

BOTULUS Guiart, 1938   [T(w,s); t(w,s)]

Profundiella A. S. Skrjabin, 1958
Mediolecithus Oshmarin, 1968

Body normally stout. Uroproct present. Testes symmetrical to oblique; in anterior hindbody;
large. Seminal vesicle thin-walled throughout its length; tubular and convoluted [or (?) globular
(in *Profundiella skrjabini* A. S. Skrjabin, 1958)]. 'Cirrus-sac' small; globular. 'Cirrus' cone-shaped
to digitiform. Genital atrium often everted through genital pore. Ovary in anterior hindbody.
Uterus reaching extra-caecally in anterior hindbody. Vitellarium a densely tangled mass of
tubeles in one ventral, inter-caecal field between ovary and posterior extremity. Parasitic in
stomach of large, carnivorous, marine teleosts (*Alepisaurus*) and (?) accidentally in piscivorous
sharks.

TYPE-SPECIES. *Botulus microporus* (Monticelli, 1889) [syn. *B. alepidosauri* Guiart, 1938 – type by
monotypy].

COMMENT. The two specimens of *Botulus alepidosauri* originally described by Guiart (1938),
according to his manuscript, were in poor condition (they were dried out) which accounts for the
inadequate description. We have been able to examine specimens of *Botulus* from the type-host,
Alepisaurus ferox, and to refine the concept of this genus (see Gibson & Bray, 1977). We have
also examined the type-specimens of *Distomum microporum* Monticelli, 1889, present in the
collections of the British Museum (Natural History). These specimens were recovered from the
type-host (*A. ferox*) and type-locality (off Madeira) of *B. alepidosauri*. Although *D. microporum*
has been listed as a species of *Hemiurus* by some authors (Looss, 1899; Yamaguti, 1971), our
examination has convinced us that it is a senior synonym of *B. alepidosauri*. The morphology of
Botulus microporus is described in detail elsewhere (Gibson & Bray, 1977).
    Profundiella was originally erected for a new species, *P. skrjabini*, from *Alepisaurus aesculapius*
(which may be synonymous with *A. ferox*), in the Pacific Ocean by A. S. Skrjabin (1958). There
appears to be no significant difference between this genus and *Botulus*, except for the reported
presence of a globular seminal vesicle in the former. A second species, *P. alepisauri*, was described
by Parukhin & Nikolaeva (1967) from *Alepisaurus* sp. in the Gulf of Mexico (*A. ferox* appears to
be the only species of *Alepisaurus* recorded in this region); but this species possesses a seminal
vesicle which is tubular and coiled. Examination of specimens of *Botulus* from *Alepisaurus ferox*

from off Miami Beach, Florida, show that they appear to be indistinguishable from *B. microporus*. It seems probable that the apparent globular seminal vesicle of *P. skrjabini* may in fact be a tightly coiled, tubular form, as a tubular seminal vesicle is the normal condition in primitive hemiuroids. Stunkard (1965) also considered *Profundiella* as a synonym of *Botulus*, but it was listed separately by Yamaguti (1971).

In agreement with Parukhin & Nikolaeva (1974), we are of the opinion that *Mediolecithus pacificus* Oshmarin, 1968, belongs to *Botulus*. One specimen was described by Oshmarin from *Lamna cornubica*, a piscivorous shark. It is likely that this was an accidental infestation, as *Alepisaurus* is the normal host of *Botulus*.

LAMPRITREMA Yamaguti, 1940 [T(s)]

Hirudinelloides Gaevskaja & Kovaleva, 1977

Body elongate; slender. Papillae present on forebody. Uroproct absent. Testes in tandem; near middle of hindbody. Most of seminal vesicle thin-walled, but distal portion forms thick-walled, muscular 'pars musculosa'. Thick-walled pars prostatica lies ventral to posterior portion of 'cirrus-sac'. Male duct leads into 'cirrus-sac' some distance from its posterior extremity. 'Cirrus-sac' large; elongate; club-shaped. 'Cirrus' long or short; capable of being extruded some distance through genital pore. Genital atrium deep. Ovary near middle of hindbody. Laurer's canal (?) absent. Seminal receptacle (?) small; enclosed in Mehlis' gland [see below]. Uterus extends back to near posterior limit of vitellarium; mainly coiled inter-caecally in post- and pre-ovarian regions of hindbody. Vitellarium a pair of lateral tubules with short dorsal branches; mainly extra-caecal; passing posteriorly from ovary to about half-way to posterior extremity. Excretory arms appear to unite in forebody (cf. Yamaguti, 1940). Parasitic in stomach (? occasionally on gills) of marine teleosts (*Lampris*, *Brama* and *Thyrsites*). Immature forms recorded from salmonids (stomach, oesophagus or gills).

TYPE-SPECIES. *Lampritrema miescheri* (Zschokke, 1890) [syn. *L. nipponicum* Yamaguti, 1940 – type by original designation].

COMMENT. We considered separating *Lampritrema* from *Hirudinella* and *Botulus* at the subfamily level, but there are no morphological differences which one could definitely consider to be important at the subfamily level.

Notwithstanding the descriptions of *Lampritrema atlanticum* Delyamure & Serdyukov, 1970, *L. hawaiiense* Yamaguti, 1970, and *Hirudinelloides elongatus* Gaevskaja & Kovaleva, 1977, we consider this genus to be monotypic (see Gibson & Bray, 1977). *L. savalai* Zaidi & Khan, 1977, is clearly a hemiurid.

Yamaguti (1940) stated that Laurer's canal was absent in *Lampritrema nipponicum* and that a small seminal receptacle was present inside Mehlis' gland. We question the absence of Laurer's canal in this species, as it is present in all other primitive hemiuroids, and the small size (up to 105 µm) and location of the seminal receptacle suggests that its presence and nature is questionable: we would expect a uterine seminal receptacle to be present. Neither of these features were commented upon by Margolis (1962) in his redescription of this species.

Family ISOPARORCHIIDAE Travassos, 1922

Body large; stout; dorso-ventrally flattened. Ecsoma absent. Body-surface smooth. Oral and ventral suckers small. Pharynx well developed. Oesophagus short. 'Drüsenmagen' absent. Gut-caeca sinuous; terminate blindly near posterior extremity. Testes two; symmetrical; pre-ovarian; in anterior hindbody. Seminal vesicle small; thin-walled; tubular; winding in forebody. Pars prostatica tubular. Ejaculatory duct within sinus-sac. Sinus-sac weakly developed; composed of diffuse musculature. Hermaphroditic duct short; opens into genital atrium through stout sinus-organ. Genital atrium with pair of concentric folds in its wall; capable of being extruded through genital pore [see Fig. 2]. Genital pore mid-ventral in forebody. Ovary tubular; well posterior to

testes. Laurer's canal present; may be slightly dilated proximally forming small rudimentary seminal receptacle. Uterine seminal receptacle present. Juel's organ and canalicular or blind seminal receptacle absent. Uterus pre-ovarian; mainly coiled in hindbody. Eggs numerous; small; non-filamented. Vitellarium tubular; with dendritic branches arising from about six collecting ducts; post-ovarian. Excretory vesicle Y-shaped; arms come close together dorsal to pharynx, but do not unite. Parasitic in swim-bladder of physostomatous teleosts in freshwater (Asia and Australasia).

ISOPARORCHIS Southwell, 1913   [t(w,s)]

Leptolecithum Kobayashi, 1915

Defined as family.

TYPE-SPECIES. *Isoparorchis hypselobagri* (Billet, 1898) [syn. *I. trisimilitubis* Southwell, 1913 – type by original designation].

Family **LECITHASTERIDAE** Odhner, 1905

Lobatovitelliovariidae Yamaguti, 1965

Body usually small; normally spindle-shaped, occasionally elongate. Ecsoma absent. Body-surface smooth. Oral and ventral suckers well developed; ventral sucker normally in anterior half of body. Muscular flange or flanges may be present immediately posterior to ventral sucker. Pharynx well developed. Oesophagus usually short. 'Drüsenmagen' normally present. Gut-caeca usually terminate blindly, but occasionally unite forming cyclocoel. Presomatic pit and ventro-cervical groove absent. Testes two, occasionally one; in tandem; oblique or symmetrical; usually, but not always, pre-ovarian; in hindbody. Seminal vesicle generally thin-walled, occasionally muscular; oval, tubular or constricted into portions; in fore- or hindbody. Pars prostatica usually tubular, occasionally vesicular; may be linked to seminal vesicle by aglandular tube. Ejaculatory duct long, short or absent. Hermaphroditic duct present. Ejaculatory (prostatic) vesicle absent. Sinus-sac usually present; well or poorly developed; occasionally absent. Permanent sinus-organ normally absent, but hermaphroditic duct is often protruded to form temporary sinus-organ. Genital atrium large, small or absent. Ovary usually post-testicular; oval or four- (occasionally three-) lobed. Usually only blind seminal receptacle present (normally large, thick-walled and situated dorsal or antero-dorsal to ovary) and Laurer's canal, Juel's organ and both uterine or canalicular seminal receptacles absent; occasionally only Juel's organ and uterine seminal receptacle present; rarely only Laurer's canal and canalicular seminal receptacle present. Uterus mainly post- to entirely pre-ovarian; main bulk rarely extends into forebody. Eggs numerous; small; rarely filamented. Vitellarium commonly seven-lobed; occasionally six, eight or double these numbers (sometimes branched) lobes often in rosette arrangement; usually immediately post-ovarian, occasionally pre-ovarian or at level of ovary. Excretory vesicle Y-shaped; arms united in forebody or not. Parasitic in gut, especially intestine, of marine teleosts.

Key to Lecithasteridae

1. A. Uterine seminal receptacle present   .   .   .   .   . **HYSTEROLECITHINAE** (p. 104)
   B. Uterine seminal receptacle absent   2
2. A. Uterus entirely or almost entirely pre-ovarian; hermaphroditic duct appears to be
      continuation of uterus; Laurer's canal may be present   .   **TRIFOLIOVARIINAE** (p. 109)
   B. Uterus partly post-ovarian; hermaphroditic duct normal   3
3. A. Muscular ventro-lateral flange or flanges present immediately posterior to ventral sucker
                                                                  QUADRIFOLIOVARIINAE (p. 108)
   B. Muscular ventro-lateral flange or flanges absent immediately posterior to ventral sucker   . 4
4. A. Seminal vesicle in forebody or dorso-lateral to ventral sucker (in one or two species of
      Lecithaster it may extend into the anterior hindbody, but these can be distinguished
      from the macradeninines by the well-developed nature of the sinus-sac)   .   .   . 5

B.   Seminal vesicle entirely in hindbody; pars prostatica and/or ejaculatory duct long; sinus-sac small or poorly developed; usually parasitic in *Acanthurus* spp.
MACRADENININAE (p. 105)
5. A.   Sinus-sac relatively well developed; vitellarium post-ovarian .   **LECITHASTERINAE** (p. 102)
B.   Sinus-sac apparently absent; genital atrium sucker-like; vitellarium pre-ovarian
PROLECITHINAE (p. 107)

Subfamily **LECITHASTERINAE** Odhner, 1905

Lecithophyllinae Skrjabin & Guschanskaja, 1954

Caeca terminate blindly. Testes two, occasionally one; pre-ovarian. Seminal vesicle in forebody, dorsal to ventral sucker or, occasionally, in anterior hindbody. Pars prostatica short to medium in length. Ejaculatory duct absent or short. Sinus-sac well developed. Permanent sinus-organ absent. Ovary entire or four-lobed. Blind seminal receptacle normally large; usually dorsal to ovary. Uterus reaches to post-ovarian region. Vitellarium seven (rarely six or eight) oval to digitiform lobes in rosette or two linked groups of three and four; immediately post-ovarian; occasionally antero-posteriorly oriented. Excretory arms united in forebody or not. Normally parasitic in intestine or stomach of marine teleosts.

Key to Lecithasterinae

1. A.   Testis single   .   .   .   .   *MONORCHIAPONURUS*
B.   Testes two   2
2. A.   Vitelline lobes tubular   .   .   .   .   .   .   *QADRIANA* (inadequately described)
B.   Vitelline lobes tear-shaped to globular   3
3. A.   Ovary lobed, usually with four lobes; vitelline lobes tear-shaped .   .   .   *LECITHASTER*
B.   Ovary oval to globular; vitelline lobes globular   4
4. A.   Genital atrium present   .   .   .   .   *LECITHOPHYLLUM*
B.   Genital atrium small or absent   .   .   .   .   *APONURUS*

LECITHASTER Lühe, 1901   [n(w,s)]

Testes two; obliquely symmetrical; usually oval, but occasionally lobed. Seminal vesicle saccular to elongate and sinuous; in forebody, dorsal to ventral sucker or, occasionally, in anterior hindbody. Sinus-sac oval. Genital atrium short. Ovary normally four-lobed. Seminal receptacle large, globular; dorsal to ovary. Vitellarium a radiating mass of seven tear-shaped lobes. Excretory arms apparently not united in forebody. Parasitic in intestine of marine teleosts.

TYPE-SPECIES. *Lecithaster confusus* Odhner, 1905 [by subsequent designation – Odhner, 1905].

COMMENT. Dawes (1947) lists *Leptosoma* Stafford, 1904 [*nec* Desmarest, 1825; *nec* Travassos, 1920; etc.; etc.] as a synonym of *Lecithaster*; but Stafford's description of *Leptosoma obscurum* is not adequate for a determination, even at the family-level. For this reason, therefore, and because: (1) *Leptosoma* was not mentioned by Miller (1941), who studied Stafford's material; (2) there are no specimens amongst Stafford's material in the National Museums of Canada, Ottawa; and (3) lecithasterids do not appear to be normal parasites of *Lophius*, from which *Leptosoma* was recorded; we consider that this genus is unrecognizable.

APONURUS Looss, 1907

Brachadena Linton, 1910
(?) *Mordvilkoviaster* Pigulewsky, 1938

Testes two; tandem to oblique. Seminal vesicle saccular; in forebody or occasionally dorsal to ventral sucker. Hermaphroditic duct usually tubular, occasionally bipartite. Sinus-sac oval to

elongate-oval. Genital atrium absent, or occasionally small. Ovary oval or globular. Seminal receptacle small to large; (?) ventral or dorsal to anterior region of ovary. Vitellarium usually seven globular to slightly elongate lobes; in lateral, occasionally antero-posteriorly oriented, groups of three and four. Excretory arms united in forebody. Parasitic in stomach (occasionally intestine) of marine teleosts.

TYPE-SPECIES. *Aponurus laguncula* Looss, 1907 [by monotypy].

COMMENT. The validity of *Aponurus* as a distinct genus from *Lecithophyllum* has been a matter of some discussion (see Margolis, 1958). The two genera differ in the presence and absence of a distinct genital atrium. As this is a contractile organ, its use as an important taxonomic criterion should be treated with caution. In this case the character does appear to be of value, as it is a deep and apparently consistent feature in species of *Lecithophyllum*. It would not be surprising, however, if future workers discovered that, with regard to this feature, the two genera tend to grade into one another: indeed, *Lecithophyllum hawaiiense* Yamaguti, 1970, may be such a case in point. Yamaguti (1953) used the nature of the hermaphroditic duct to distinguish these two genera: species of *Lecithophyllum* normally possess an hermaphroditic duct which is bipartite, whereas in *Aponurus* it is supposed to be uniform throughout its length. Yamaguti's (1970) figure of *Aponurus acanthuri* Manter & Pritchard, 1960, which he placed in *Lecithophyllum* despite the extremely small size of the genital atrium, and Overstreet's (1973) figure of *A. pyriformis* (Linton, 1910) indicate that these species have bipartite hermaphroditic ducts.

With regard to the status of *Brachadena* Linton, 1910, Yamaguti (1953, 1958, 1971) considered this genus a synonym of *Lecithophyllum*, whereas Margolis (1958) believed it to be distinct on the basis of a central union of the vitelline lobes. Contrary to the work of Fischthal & Kuntz (1964c), which showed that a small genital atrium is present in the type-species, *B. pyriformis* Linton, 1910, Overstreet (1973) demonstrated that there is no distinct genital atrium present: Yamaguti's (1971) figure of the paratype also indicated that there is no genital atrium present. Overstreet's work showed that the type-species has an antero-posteriorly oriented vitellarium, the three- and four-lobed groups of which being united by a short duct. In view of the questionable validity of *Aponurus* itself, we feel that any variations in the nature and orientation of the vitellarium and in the hermaphroditic duct of *Brachadena pyriformis*, as compared with other species of *Aponurus*, should be regarded as being of only specific value.

Aponurus priacanthi Yamaguti, 1970, does not appear to be a lecithasterine. A uterine seminal receptacle and possibly a Juel's organ are shown in Yamaguti's figure of this species.

We have tentatively included *Mordvilkoviaster* Pigulewsky, 1938, as a synonym of *Aponurus*, as both Looss (1908) and Pogoreltseva (1952) have described *Lecithaster galeatus* Looss, 1907, the type-species, as having a round ovary. Skrjabin & Guschanskaja (1954) and Yamaguti (1971) consider *Mordvilkoviaster* to be a synonym of *Dichadena* Linton, 1910; but we believe that the sinus-sac is too well developed, the seminal vesicle too anterior and the pars prostatica too short for it to be considered a macradeninine.

LECITHOPHYLLUM Odhner, 1905   [t(w,s)]

Testes two; obliquely tandem to symmetrical. Seminal vesicle saccular; in forebody or dorsal to ventral sucker. Hermaphroditic duct apparently bipartite. Sinus-sac elongate. Genital atrium present; generally deep. Ovary oval or globular. Seminal receptacle large; dorsal to ovary. Vitellarium seven globular lobes, in lateral groups of three and four. Excretory arms united in forebody. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Lecithophyllum botryophoron* (Olsson, 1868) [by original designation].

COMMENT. Brinkmann (1977), in his detailed redescription of the type-species, described and figured a sinus-organ. As with other species in this family, this structure is temporary: it is not present in our material of this species (fixed in glacial acetic acid). A temporary sinus-organ, however, can be extruded in artificially relaxed, slowly fixed or frozen material.

(?) *MONORCHIAPONURUS* Fischthal & Nasir, 1974

Testis single. Seminal vesicle saccular; in forebody. Sinus-sac elongate. Hermaphroditic duct tubular. Genital atrium absent. Ovary oval. Seminal receptacle pre-ovarian; postero-dextral to testis. Vitellarium seven globular lobes. Parasitic in intestine of marine teleosts.

TYPE-SPECIES. *Monorchiaponurus hemirhamphi* Fischthal & Nasir, 1974 [by original designation].

COMMENT. This genus is known from only one specimen. As the absence of one testis is not a rare feature amongst bi-testicular digeneans, it is possible that this specimen is merely an abnormal example of *Aponurus*. More specimens, as in the case of *Monorchimacradena* Nahhas & Cable, 1964, are required before this genus can be fully accepted. In listing this genus independently of *Aponurus*, we are assuming that the seminal receptacle, which is rather far anterior for a lecithasterid, has not been confused with the second testis.

(?) *QADRIANA* Bilqees, 1971

[Inadequately described.] Testes two; tandem; postero-lateral to ventral sucker. Seminal vesicle saccular; in forebody. Ovary oval. 'Seminal receptacle not obvious.' Vitellarium 'composed of several tubes'. Uterus extra-caecal in hindbody. Parasitic in stomach of marine teleosts.

TYPE-SPECIES. *Qadriana fusiformis* Bilqees, 1971 [by monotypy].

Subfamily **HYSTEROLECITHINAE** Yamaguti, 1958

Body small; elongate to spindle-shaped. Ventral sucker in middle or anterior half of body. Gut-caeca end blindly near posterior extremity. Testes two; oval; symmetrical to obliquely tandem; pre-ovarian; in anterior half of hindbody. Seminal vesicle usually tubular, occasionally elongate saccular; in forebody. Pars prostatica usually tubular, occasionally vesicular; short. Sinus-sac present; often weakly developed; occasionally of open-type. Permanent sinus-organ absent; temporary sinus-organ may form. Hermaphroditic duct present within sinus-sac. Genital atrium small or absent. Ovary oval; in anterior or posterior half of hindbody. Laurer's canal and blind or canalicular seminal receptacle absent. Juel's organ and uterine seminal receptacle present [see below]. Uterus almost entirely in hindbody; mainly pre- to mainly post-ovarian. Eggs with or without filaments. Vitellarium seven (occasionally eight) oval to digitiform lobes; post-ovarian. Excretory arms united in forebody or not. Parasitic mainly in intestine or stomach of marine teleosts (usually perciform genera, especially acanthurids and pomacentrids).

COMMENT. There appears to have been some confusion between the genera of this subfamily and certain other lecithasterid genera. We have, therefore, taken our definitions only from species in which the presence of a uterine seminal receptacle or the absence of a blind or canalicular seminal receptacle has been indicated. Although Juel's organ has not been reported previously in this group, we found it to be well developed in a paratype specimen of *Hysterolecitha elongata* Manter, 1931, from the H. W. Manter Collection, which Dr M. H. Pritchard kindly allowed us to section. Yamaguti (1934) in his description of *Hysterolecithoides epinepheli* referred to a large seminal receptacle in addition to a uterine seminal receptacle, and in his (1942) description of *Hysterolecitha nahaensis* he referred to a small seminal receptacle in addition to a uterine seminal receptacle. Unless a similar variation to that present in the Derogeninae occurs in this subfamily, it is probable that the organ described by Yamaguti as a seminal receptacle is Juel's organ.

Key to Hysterolecithinae

1. A. Eggs filamented .   .   .   .   *THULINIA*
   B. Eggs without filaments   2
2. A. Excretory arms united in forebody; uterus mainly pre-ovarian .   .   *HYSTEROLECITHA*
   B. Excretory arms not united in forebody; uterus mainly post-ovarian *HYSTEROLECITHOIDES*

COMMENT. In order to identify a genus from this subfamily, it is essential that eggs are teased from the body and that the anterior regions of the excretory system are examined. The latter normally necessitates sectioning. It is clear, in species where the excretory system has not been fully described, that there has been some confusion between *Hysterolecitha* and *Hysterolecithoides*. For example, although the excretory system was not fully described, Yamaguti (1971) placed *Hysterolecithoides pseudorosea* Bravo-Hollis, 1956, in the genus *Hysterolecitha*, despite the position of the ovary and the distribution of the uterus which suggested that Bravo-Hollis (1956) was correct.

HYSTEROLECITHA Linton, 1910   [n(w,s)]

Ventral sucker usually in anterior half of body; occasionally near middle. Seminal vesicle normally tubular; occasionally elongate saccular. Pars prostatica tubular; occasionally vesicular. Sinus-sac present; often weakly developed; may be of 'open'-type. Ovary normally in posterior half of hindbody; normally separated from testes by loops of uterus. Uterus usually mainly pre-ovarian; (?) occasionally mainly post-ovarian. Eggs without filaments. Excretory arms united in forebody.

TYPE-SPECIES. *Hysterolecitha rosea* Linton, 1910 [by original designation].

HYSTEROLECITHOIDES Yamaguti, 1934

Ventral sucker in middle of body. Seminal vesicle tubular. Pars prostatica tubular or vesicular. Sinus-sac oval. Ovary close to testes. Uterus mainly post-ovarian. Eggs without filaments. Excretory arms not united in forebody.

TYPE-SPECIES. *Hysterolecithoides epinepheli* Yamaguti, 1934 [by original designation].

THULINIA gen. nov.

Body elongate. Ventral sucker in anterior half of body. Gut-caeca end blindly near posterior extremity. Testes two; oval; obliquely tandem; separated from ventral sucker and ovary by loops of uterus. Seminal vesicle tubular; in forebody; may reach dorsally to ventral sucker. Pars prostatica tubular; short. Sinus-sac present; well developed. Permanent sinus-organ absent; temporary sinus-organ may form. Hermaphroditic duct present within sinus-sac. Genital atrium small. Genital pore mid-ventral near middle of forebody. Ovary oval; in posterior half of hindbody. Laurer's canal presumed absent. Canalicular or blind seminal receptacle absent. Juel's organ and uterine seminal receptacle presumed present. Uterus almost entirely in hindbody; coiled in pre- and post-ovarian fields. Eggs filamented (one filament at each end). Vitellarium seven (or eight) digitiform lobes; post-ovarian. Excretory vesicle Y-shaped; excretory arms united in forebody. Parasitic in intestine of marine teleosts.

TYPE-SPECIES. *Thulinia tinkeri* (Manter & Pritchard, 1960) n. comb.

COMMENT. We have erected this genus because of the presence of filaments on the eggs, a feature which we believe to be a good generic criterion. It is named after Mr Jan Thulin, University of Gothenburg, who has helped us with several aspects of our work.

Subfamily **MACRADENININAE** Skrjabin & Guschanskaja, 1954

Gut-caeca usually end blindly, but cyclocoel sometimes present. Testes two, occasionally one; oval; usually pre-ovarian, but may be at level of ovary or post-ovarian. Seminal vesicle in hindbody; saccular, tri-partite or tubular. Pars prostatica tubular; long. Ejaculatory duct usually long, but may be short or absent. Sinus-sac present; small; may be poorly developed. Permanent sinus-organ absent. Ovary four-lobed or oval. Blind seminal receptacle present. Uterus reaches to post-ovarian region. Vitellarium immediately anterior, at level of or immediately posterior to ovary; variable, commonly six- to eight-lobed, but may be seven branched lobes, or twelve or

fourteen lobes, and group of lobes may be antero-posteriorly oriented. Excretory arms united in forebody or not. Parasitic in intestine or stomach of marine teleosts (normally *Acanthurus* spp.).

Key to Macradenininae

1. A. Vitellarium consisting of 6 to 8 (usually 7) tear-shaped or slightly branched lobes; seminal
    vesicle saccular (? or tubular) 2
  B. Vitellarium consisting of 12 or more lobes (occasionally 7 basic lobes divided into about
    40 secondary lobes) which may be tubular or globular; seminal vesicle tubular or
    tri-partite 5
2. A. Ovary 4-lobed . . . . *PSEUDODICHADENA*
  B. Ovary unlobed 3
3. A. Testis single . . . . *MONORCHIMACRADENA*
  B. Testes 2. 4
4. A. Testes at level of ovary; vitellarium antero-lateral to ovary; seminal vesicle (?) saccular or
    (?) tubular . . . . *DICHADENA*
  B. Testes pre-ovarian; vitellarium post-ovarian; seminal vesicle saccular (? with constriction)
    NEODICHADENA
5. A. Seminal vesicle tubular; vitelline lobes elongate, in single group 6
  B. Seminal vesicle tri-partite; vitelline lobes globular, in 2 groups, 7 anterior and 7 posterior
    to ovary . . . . *ACANTHURITREMA*
6. A. Testes post-ovarian; vitellarium 12 claviform lobes, ventral to ovary . *MACRADENINA*
  B. Testes pre-ovarian; vitellarium essentially 7 lobes, but divided into about 40 secondary
    lobes, between ovary and seminal vesicle . . . . . . *MACRADENA*

COMMENT. We have retained all of the genera in this subfamily because of conflicting accounts of their morphology and in view of Yamaguti's (1971) examination of many of the holotypes; but it is likely that some of these forms will prove to be synonymous. Several of the genera require the study of fresh material before their validity can be confirmed, and a redescription of *Dichadena acuta* Linton, 1910, especially is needed. This subfamily appears to be almost entirely restricted to fishes of the genus *Acanthurus* from the central American region and Hawaii.

MACRADENINA Manter, 1947

Cyclocoel not reported. Testes tandem; post-ovarian. Seminal vesicle tubular; loosely coiled at level of ovary. Pars prostatica long. Ejaculatory duct (?) absent. Sinus-sac sub-cylindrical; may be incomplete posteriorly; appears to be protrusible. Ovary four-lobed; well forward in hindbody. Seminal receptacle globular; large; post-ovarian. Vitellarium twelve claviform, unbranched tubules; ventral to ovary. Excretory arms (?).

TYPE-SPECIES. *Macradenina acanthuri* Manter, 1947 [by original designation].

ACANTHURITREMA Yamaguti, 1970

Cyclocoel not reported. Testes tandem to oblique; pre-ovarian. Seminal vesicle tri-partite; posterior part large and spherical, middle part elongate elliptical, anterior part pyriform; connected to pars prostatica by aglandular duct; in anterior hindbody. Pars prostatica short. Ejaculatory duct absent. Sinus-sac thin, membranous; indistinct. Ovary four-lobed. Seminal receptacle large; antero-dorsal to ovary. Vitellarium fourteen globular lobes; seven anterior and seven posterior to ovary. Excretory arms not united in forebody.

TYPE-SPECIES. *Acanthuritrema multivitellosum* Yamaguti, 1970 [by original designation].

DICHADENA Linton, 1910

Cyclocoel (?) not reported (except in key by Yamaguti, 1971). Testes tandem; dorsal to ovary. Seminal vesicle sac-like (tubular according to Yamaguti, 1971); immediately pre-testicular. Pars

prostatica long; dilate posteriorly. Ejaculatory duct similar in length to pars prostatica. Sinus-sac oval. Ovary oval [four-lobed according to Manter, 1947: specimens with four-lobed ovary described by Siddiqi & Cable, 1960, as *D. acuta*, now placed in *Pseudodichadena*]. Seminal receptacle between posterior margin of ovary and posterior testis. Vitellarium six or seven rounded to tear-shaped lobes; antero-lateral to ovary. Excretory arms (?).

TYPE-SPECIES. *Dichadena acuta* Linton, 1910 [by original designation].

MACRADENA Linton, 1910

Cyclocoel not reported. Testes tandem; pre-ovarian. Seminal vesicle tubular; coiled in anterior hindbody. Pars prostatica long. Ejaculatory duct about one quarter length of pars prostatica. Sinus-sac weakly developed and small. Ovary four ovoid lobes. Seminal receptacle large; oval; immediately posterior to ovary. Vitellarium originates between ovary and seminal receptacle; consists of seven main radial lobes which are finely divided to form about forty fairly short, tubular lobes. Excretory arms united in forebody.

TYPE-SPECIES. *Macradena perfecta* Linton, 1910 [by original designation].

MONORCHIMACRADENA Nahhas & Cable, 1964

Cyclocoel not reported. Testis single; immediately pre-ovarian. Seminal vesicle sac-like; immediately pre-testicular. Pars prostatica and ejaculatory duct about equal in length. Sinus-sac spherical to pyriform; small. Ovary oval. Seminal receptacle as large or larger than ovary; dorsal to ovary. Vitellarium seven digitiform or slightly branched lobes; united centrally; post-testicular. Excretory arms united in forebody.

TYPE-SPECIES. *Monorchimacradena acanthuri* Nahhas & Cable, 1964 [by original designation].

NEODICHADENA Yamaguti, 1971

Cyclocoel not reported. Testes oblique; immediately pre-ovarian. Seminal vesicle sac-like (may have constriction). Pars prostatica long. Ejaculatory duct about half length of pars prostatica. Sinus-sac small; spherical. Ovary oval. Seminal receptacle large; lateral to ovary. Vitellarium about eight tear-shaped lobes; post-ovarian. Excretory arms united in forebody.

TYPE-SPECIES. *Neodichadena acanthuri* (Siddiqi & Cable, 1960) [by original designation].

PSEUDODICHADENA Yamaguti, 1971

Cyclocoel present. Testes small; tandem; at level of ovary. Seminal vesicle elliptical; dorsal at level of gonads. Pars prostatica long. Ejaculatory duct short. Sinus-sac oval. Ovary four-lobed. Seminal receptacle post-ovarian. Vitellarium seven tear-shaped lobes; antero-lateral to ovary. Excretory arms united in forebody.

TYPE-SPECIES. *Pseudodichadena lobata* Yamaguti, 1971 [syn. *Dichadena acuta* of Siddiqi & Cable, 1960, *nec* Linton, 1910] [by original designation].

Subfamily **PROLECITHINAE** Yamaguti, 1971

Folliovitellotrematinae Gupta & Sharma, 1972 (*sic*)

Body spindle-shaped. Ventral sucker large, prominent. Cyclocoel present. Testes two; diagonal to symmetrical; at level of or slightly posterior to ventral sucker. Seminal vesicle saccular; in forebody. Pars prostatica short; vesicular. Sinus-sac and permanent sinus-organ absent. Large, spherical genital atrium present with muscular walls forming sucker-like structure (it is possible that this structure is an hermaphroditic duct surrounded by the remains of a sinus-sac). Ovary three- to four-lobed; near posterior extremity; overlying cyclocoel. Blind seminal receptacle

posterior to ovary; at posterior extremity of body. Uterus mainly anterior to gonads. Vitellarium seven rounded lobes; immediately pre-ovarian; close to testes. Excretory arms not united in forebody. Parasitic in intestine of marine teleosts (Belonidae).

PROLECITHA Manter, 1961

Lobatovitelliovarium Yamaguti, 1965
Follicovitellosum Gupta & Sharma, 1972

As subfamily.

TYPE-SPECIES. *Prolecitha obesa* Manter, 1961 [by original designation].

Subfamily **QUADRIFOLIOVARINAE** Yamaguti, 1970

Body elongate to spindle-shaped. Muscular ventro-lateral flange or flanges present immediately posterior to ventral sucker. Caeca usually terminate blindly, but cyclocoel may be present. Testes two; pre-ovarian. Seminal vesicle in hindbody; saccular, constricted into portions or tubular. Pars prostatica usually short; tubular; in hindbody. Ejaculatory duct long; may be lined with cuticular villi. Sinus-sac oval. Permanent sinus-organ absent. Genital atrium short or apparently absent. Ovary oval or four-lobed. Blind seminal receptacle normally large; anterior or antero-dorsal to ovary. Uterus reaches to post-ovarian region. Vitellarium seven post-ovarian, claviform or oval lobes, or two groups of six to seven digitiform lobes, one pre-ovarian and one post-ovarian. Excretory arms united in forebody. Parasitic in stomach or pyloric caeca of acanthurid marine teleosts.

COMMENT. This subfamily is morphologically similar to the Macradenininae, differing fundamentally only in the presence of muscular flanges just posterior to the ventral sucker and in the length of the pars prostatica. It is worth noting that all of the macradeninine and quadrifoliovariine genera are parasitic in acanthurid teleosts.

Key to Quadrifoliovariinae

1. A. Muscular ventro-lateral flange present on one side of body only; cyclocoel present
   UNILACINIA
   B. Muscular ventro-lateral flanges symmetrical; cyclocoel absent 2
2. A. Ovary 4-lobed; vitelline lobes in 2 antero-posteriorly oriented groups
   QUADRIFOLIOVARIUM
   B. Ovary oval; vitelline lobes in one group . . . . *BILACINIA*

QUADRIFOLIOVARIUM Yamaguti, 1965

Pair of muscular ventro-lateral flanges immediately posterior to ventral sucker. Cyclocoel not reported. Testes tandem. Seminal vesicle a wide, convoluted tube; narrowing anteriorly. Pars prostatica short. Ejaculatory duct two to three times length of pars prostatica. Hermaphroditic duct convoluted; may be everted to form temporary sinus-organ. Sinus-sac thin-walled; elliptical to oval. Ovary four-lobed. Vitellarium in two antero-posteriorly oriented rosette-like groups; one pre- and one post-ovarian; united by collecting duct; each group has six or seven digitiform lobes. Parasitic in stomach and pyloric caeca of marine teleosts (*Naso*).

TYPE-SPECIES. *Quadrifoliovarium pritchardae* Yamaguti, 1965 [by original designation].

BILACINIA Manter, 1969

Holacanthitrema Yamaguti, 1970

Pair of bilobed, muscular ventro-lateral flanges; symmetrical; immediately posterior to ventral sucker. Cyclocoel not reported. Testes tandem to oblique. Seminal vesicle convoluted, wide and

tubular or divided into four to five portions. Pars prostatica sigmoid. Ejaculatory duct one quarter to nearly equal length of pars prostatica. Hermaphroditic duct wide; straight. Sinus-sac oval; thin-walled. Ovary oval. Vitellarium seven rounded to claviform lobes; immediately post-ovarian. Parasitic in stomach and pyloric caeca of marine teleosts (*Naso* and *Holacanthus*).

TYPE-SPECIES. *Bilacinia australis* Manter, 1969 [by original designation].

UNILACINIA Manter, 1969

Bilobed muscular flange lateral to ventral sucker, on one side only. Cyclocoel present. Testes oblique. Seminal vesicle saccular; antero-dorsal to anterior testis. Ejaculatory duct twice length of pars prostatica. Hermaphroditic duct wide. Sinus-sac broadly ovoid. Ovary oval. Vitellarium seven short, digitiform lobes; postero-ventral to ovary. Parasitic in stomach of marine teleosts (*Naso*).

TYPE-SPECIES. *Unilacinia asymmetrica* Manter, 1969 [by original designation].

Subfamily **TRIFOLIOVARIINAE** Yamaguti, 1958

Body cylindrical; long and thin, fusiform or elongate oval. Ventral sucker present well inside anterior half of body. Gut-caeca terminate blindly; often wide. Testes two; pre-ovarian in anterior hindbody; separated from ovary by many loops of uterus. Seminal vesicle in forebody, at level of ventral sucker or in hindbody; tubular, moniliform or elongate oval. Pars prostatica short; tubular or vesicular. Ejaculatory duct short; enters hermaphroditic duct, which is continuation of uterus, laterally. Sinus-sac present surrounding hermaphroditic duct; weak and membranous; tubular or oval. Permanent sinus-organ absent. Genital atrium absent or small. Female reproductive complex close to posterior extremity. Ovary four-lobed. Laurer's canal present or absent. Seminal receptacle large; blind or canalicular; dorsal or antero-dorsal to ovary. Uterine seminal receptacle and Juel's organ absent. Uterus entirely or almost entirely pre-ovarian; coils confined to hindbody. Eggs without filaments. Vitellarium seven or eight claviform or digitiform lobes, which may be bilobed or irregularly branched distally; at level of ovary or immediately post-ovarian. Excretory arms united in forebody. Parasitic in intestine of marine teleosts.

Key to Trifoliovariinae

1. A. Body long and thin; seminal vesicle in hindbody or dorsal (to antero-dorsal) to ventral sucker, elongate oval (to tubular and sinuous); vitelline lobes claviform, unbranched, in rosette arrangement; Laurer's canal present   .   .   .   . **TRIFOLIOVARIUM**
   B. Body elongate oval to fusiform; seminal vesicle in forebody or antero-dorsal to ventral sucker, tubular, moniliform or elongate oval; Laurer's canal absent [or at least not reported]   2
2. A. Seminal vesicle elongate oval; vitellarium a rosette of 12 to 16 lobes (possible ca. 7 bilobed lobes); pars prostatica vesicular   .   .   .   .   .   . **PSEUDOLECITHASTER**
   B. Seminal vesicle tubular or moniliform   3
3. A. Uterus mainly intercaecal; vitellarium 2 groups of 4 unbranched posteriorly oriented tubular lobes; seminal vesicle moniliform, antero-dorsal to ventral sucker   . **ASSITREMA**
   B. Uterus reaches extracaecally; vitellarium a rosette arrangement of 7 short tubular distally branched lobes; seminal vesicle tubular, in forebody   .   . **CLADOLECITHOTREMA**

TRIFOLIOVARIUM Yamaguti, 1940   [T(w)]

Body long and thin. Oral sucker funnel-shaped. Testes tandem to oblique; widely separated. Seminal vesicle elongate oval (or tubular and sinuous); in hindbody or dorsal to ventral sucker (or antero-dorsal to ventral sucker); connected to pars prostatica by short, aglandular duct. Pars prostatica tubular. Sinus-sac tubular. Laurer's canal present, uniting canalicular seminal receptacle with dorsal surface. Vitellarium seven claviform lobes at level of ovary.

TYPE-SPECIES. *Trifoliovarium acanthocepolae* Yamaguti, 1940 [by original designation].

COMMENT. Yamaguti (1940) originally described the ovary as being three-lobed; hence the generic name, but later (1971) corrected this observation to four-lobed. Having examined the type-material of *T. acanthocepolae*, we can confirm this emendation.

The information given above in parentheses is taken from the descriptions of *T. triacanthi* Bilqees, 1973, and *T. triacanthusi* Gupta & Ahmad, 1976. These species, which are probably synonymous, were described from *Triacanthus* spp. off the Indian sub-continent.

ASSITREMA Parukhin, 1976

Body small; oval to elongate oval. Gut-caeca wide. Testes symmetrical; separated by coils of uterus. Seminal vesicle short, moniliform; winding antero-dorsally to ventral sucker. Pars prostatica tubular (but wider in middle according to figure). Sinus-sac small; oval. Laurer's canal (?). Seminal receptacle (? blind or canalicular) present. Uterus almost entirely pre-ovarian; mainly inter-caecal. Eggs small. Vitellarium two symmetrical groups of four postero-laterally oriented, digitiform lobes; centre of each group immediately post-ovarian. Excretory arms (?).

TYPE-SPECIES. *Assitrema eichleri* Parukhin, 1976 [by original designation].

COMMENT. Parukhin's (1976c) figure indicates that the hermaphroditic duct is a continuation of the ejaculatory duct. In the other three genera of this subfamily the hermaphroditic duct is a continuation of the metraterm. This may be just a matter of interpretation, for there is no evidence that Parukhin sectioned either of his two specimens. There is a possibility, if the two specimens of *Assitrema* were young, that some of the differences between this genus and *Cladolecithotrema* are the result of age. This question cannot be resolved until further material of *Assitrema* is studied.

CLADOLECITHOTREMA Ichihara, 1970   [T(w,s)]

Body elongate oval. Gut-caeca wide. Testes oblique; widely separated. Seminal vesicle tubular; convoluted in forebody. Pars prostatica tubular. Sinus-sac small; oval. Laurer's canal absent. Blind seminal receptacle present. Uterine field reaches extra-caecally. Vitellarium a rosette arrangement of seven digitiform, distally branched lobes; centre immediately post-ovarian.

TYPE-SPECIES. *Cladolecithotrema callionymi* Ichihara, 1970 [by original designation].

COMMENT. We do not agree with Gupta & Sharma's (1975) proposed synonymy of *Cladolecithotrema* and *Trifoliovarium*. We consider that the shape and position of the seminal vesicle, the shape of the vitellarium and the absence or presence of Laurer's canal are sufficient criteria to distinguish these taxa.

PSEUDOLECITHASTER Campbell & Munroe, 1977

Body fusiform. Testes symmetrical; separated by coils of uterus. Seminal vesicle elongate oval; in forebody; connected to pars prostatica by short aglandular duct. Pars prostatica vesicular. Sinus-sac small; elongate oval. Ovary 'several irregular lobes' (four visible in figure). Laurer's canal (?). Seminal receptacle (?). Vitellarium a rosette of twelve to sixteen lobes (figure suggests ca. seven bilobed lobes); at level of ovary.

TYPE-SPECIES. *Pseudolecithaster antimorae* Campbell & Munroe, 1977 [by original designation].

Family **PTYCHOGONIMIDAE** Dollfus, 1937

Body medium sized; oval. Ecsoma absent. Body-surface smooth, without spines or plications. Oral and ventral suckers well developed; oral sucker larger than ventral sucker; latter situated in anterior half of body. Pharynx well developed. Oesophagus short. 'Drüsenmagen' absent. Gut-caeca form uroproct. Testes two; post-ovarian; tandem; in middle of hindbody. Seminal vesicle dilate, tubular; thin-walled; extending posteriorly into anterior hindbody. Pars prostatica

tubular. Ejaculatory and hermaphroditic duct short. Permanent sinus-organ a small cone. Sinus-sac absent. Genital atrium contains three distinct concentric folds in its wall which surround sinus-organ. Genital pore mid-ventral in forebody. Ovary oval; pre-testicular in hindbody. Mehlis' gland pre-ovarian. Laurer's canal and uterine seminal receptacle present. Juel's organ and canalicular or blind seminal receptacle absent. Uterine field extends between level posterior to testes and ventral sucker. Eggs numerous; without filaments. Vitellarium follicular; occurs in lateral fields extending throughout most of hindbody. Excretory vesicle Y-shaped; arms unite twice in forebody. Parasitic in stomach of elasmobranchs (normally carchariniform sharks).

PTYCHOGONIMUS Lühe, 1900 [t(w,s)]

Defined as family.

TYPE-SPECIES. *Ptychogonimus megastoma* (Rudolphi, 1819) [by monotypy].

COMMENT. The above definition does not take into account the description of '*Ptychogonimus megastoma*' given by Vigueras (1956), which differs from other descriptions markedly and requires confirmation.

We have examined one type-specimen (whole-mount) of *Ptychogonimus fontanus* Lyster, 1939, and consider that, although it is not in good condition, this specimen appears to be an azygiid, bearing a strong resemblance to contracted forms of *Azygia longa* (Leidy, 1851).

Family **SCLERODISTOMIDAE** Odhner, 1927

Prosogonotrematidae Vigueras, 1940
Bhaleraoiidae Srivastava, 1948
Mabiaramidae Teixeira de Freitas & Kohn, 1967

Body usually large; stout or elongate. Ecsoma absent. Body-surface smooth, but may be rugate. Oral and ventral suckers well developed; ventral sucker just posterior to middle, in middle or in anterior half of body. Pharynx well developed. Oesophagus short. 'Drüsenmagen' present or absent. Gut-caeca terminate blindly close to posterior extremity. Testes two; symmetrical, oblique or in tandem; pre-ovarian; in forebody, dorsal to ventral sucker or in anterior hindbody. Seminal vesicle tubular; convoluted or winding in forebody. Pars prostatica tubular, occasionally with wide lumen; long; convoluted or not; external gland-cells may be delimited. Ejaculatory duct present; unites with metraterm within sinus-organ forming short hermaphroditic duct. Permanent sinus-organ usually well developed; conical to cylindrical. Sinus-sac well developed, weakly developed or apparently absent. Genital atrium well developed; often almost entirely filled by sinus-organ. Genital pore mid-ventral in forebody. Ovary globular to oval; well posterior to and usually separated from testes by loops of uterus; in posterior forebody, dorsal to ventral sucker or anterior to mid-hindbody. Mehlis' gland usually posterior or postero-lateral, occasionally antero-lateral, to ovary. Laurer's canal present; opens dorsally or into rudimentary Juel's organ. Rudimentary seminal receptacle present or absent. Canalicular or blind seminal receptacle absent. Uterine seminal receptacle present. Uterus mainly in either fore- or hindbody; mainly pre- or post-ovarian. Eggs small; numerous; non-filamented. Vitellarium four to seven convoluted, tubular branches, which may subdivide; either mainly pre- or post-ovarian; either mainly in fore- or hindbody. Excretory vesicle Y-shaped; stem relatively long; arms united in forebody. Manter's organ (accessory excretory vesicle) present; single or double; dorsal to stem of excretory vesicle. Parasitic in gut (mainly stomach) (?), occasionally in body-cavity, of marine teleosts.

COMMENT. Parukhin (1976b) erected a new subfamily, the Pseudosclerodistomoidinae, within this family for *Pseudosclerodistomoides kurotchkini*, a new genus and species from the gall-bladder of *Lethrinus miniatus* in the Indian Ocean. Several features of this species, such as the position of the testes and the genital pore and the nature of the seminal receptacle, suggest that it is not a hemiuroid.

Key to Sclerodistomidae

1. A. Manter's organ double; testes in anterior hindbody   .   .   **SCLERODISTOMINAE** (p. 112)
   B. Manter's organ single; testes in forebody   2
2. A. Ovary in forebody or at level of ventral sucker; uterus and vitellarium mainly pre-ovarian
                                       PROSOGONOTREMATINAE (p. 112)
   B. Ovary in hindbody; uterus and vitellarium mainly post-ovarian   .   **PROSORCHIINAE** (p. 112)

Subfamily SCLERODISTOMINAE Odhner, 1927

Body stout. Ventral sucker near middle of body. 'Drüsenmagen' present. Testes symmetrical to oblique; in anterior hindbody. Pars prostatica long and convoluted. Sinus-sac distinctly present; musculature diffuse; surrounding base of genital atrium. Sinus-organ a stout cone. Ovary near or just anterior to middle of hindbody. Laurer's canal opens dorsally. Rudimentary seminal receptacle present. Uterus almost entirely in hindbody; mainly posterior to gonads, reaching near to posterior extremity. Vitellarium composed of convoluted, tightly helical, unbranched, filamentous tubules; commonly arranged with three on one side of body, four on other; present laterally in post-testicular region of hindbody. Manter's organ (accessory excretory vesicle) double; symmetrical. Parasitic in stomach and (?) body-cavity of marine teleosts.

SCLERODISTOMUM Looss, 1912   [t(w,s); n(w)]

Mabiarama Teixeira de Freitas & Kohn, 1967

Defined as subfamily.

TYPE-SPECIES. *Sclerodistomum italicum* (Stossich, 1893) [by monotypy].

Subfamily PROSOGONOTREMATINAE Vigueras, 1940

Body stout. Ventral sucker in middle or just posterior to middle of body. 'Drüsenmagen' absent. Testes symmetrical; in forebody. Pars prostatica long and sinuous or convoluted. Sinus-sac well developed, but composed of diffuse musculature. Sinus-organ conical to cylindrical. Ovary in forebody or at level of ventral sucker. Laurer's canal short; opens into large rudimentary Juel's organ; dilated proximally forming small rudimentary seminal receptacle. Rudimentary Juel's organ post-ovarian [distinct in sections]. Uterus mainly pre-ovarian; does not extend into hindbody. Vitellarium about three (two to four) convoluted, tubular branches on each side of body, which may subsequently divide; mainly pre-ovarian in forebody. Manter's organ (accessory excretory vesicle) single; median. Parasitic mainly in stomach of marine teleosts.

PROSOGONOTREMA Vigueras, 1940   [t(w,s)]

(?) *Bhaleraoia* Srivastava, 1948

Defined as subfamily.

TYPE-SPECIES. *Prosogonotrema bilabiatum* Vigueras, 1940 [by monotypy].

COMMENT. Nasir (1973) considers this genus to be monotypic, synonymizing seven other species with *P. bilabiatum*. We have included *Bhaleraoia* Srivastava, 1948, as a questionable synonym of this genus, because, although similar in gross morphology, it is poorly described and purported to possess a uroproct.

Subfamily PROSORCHIINAE Yamaguti, 1934

Body elongate oval to elongate. Ventral sucker normally within anterior half of body, but occasionally in middle. 'Drüsenmagen' absent. Testes tandem to almost symmetrical; in forebody or dorsal to ventral sucker. Pars prostatica broad; usually straight or arcuate; lumen wide;

external gland-cells delimited. Sinus-sac apparently absent or (?) weakly developed. Sinus-organ conical to cylindrical. Ovary in hindbody. Laurer's canal long and opening into rudimentary Juel's organ or short and opening to exterior on dorsal surface; may or may not be dilate proximally forming rudimentary seminal receptacle. Uterus mainly post-ovarian in hindbody. Vitellarium two to four branching or seven convoluted and filamentous tubules; mainly post-ovarian in hindbody; reaching near to posterior extremity. Manter's organ (accessory excretory vesicle) single; median.

Key to Prosorchiinae

1. A. Laurer's canal long, opening into rudimentary Juel's organ, dilated proximally forming
       rudimentary seminal receptacle   .   .   .   .   *PROSORCHIS*
   B. Laurer's canal short, opening dorsally to exterior; rudimentary seminal receptacle absent
                                                                     PROSORCHIOPSIS

COMMENT. These two closely related genera essentially appear to differ only in the nature of Laurer's canal. As few authors appear to have sectioned their material, many of the descriptions in the literature must be used with some degree of caution. Nevertheless, both from the literature and from our own sectioned material of *Prosorchiopsis*, it is evident that two distinct forms of Laurer's canal appear to be present.

PROSORCHIS Yamaguti, 1934

Laurer's canal long; opens distally into well-developed rudimentary Juel's organ ('terminal vesicle'); dilate proximally forming rudimentary seminal receptacle.

TYPE-SPECIES. *Prosorchis psenopis* Yamaguti, 1934 [by original designation].

COMMENT. The presence of a 'terminal vesicle' at the distal extremity of Laurer's canal has been reported in a number of descriptions of species from this genus. Considering the nature of these descriptions, especially that of Yamaguti (1934), and the structure of the related *Prosogonotrema*, we have interpreted this 'terminal vesicle' as being a rudimentary Juel's organ.

PROSORCHIOPSIS Dollfus, 1947   [t(w,s)]

Laurer's canal short; opening dorsally to exterior; distal region may be slightly dilate and possess glandular wall; rudimentary seminal receptacle absent.

TYPE-SPECIES. *Prosorchiopsis legendrei* Dollfus, 1947 [by original designation].

COMMENT. In sectioned material, part of the distal region of Laurer's canal was slightly dilate and possessed a diffuse, glandular wall (see Gibson & Bray, 1977). It is possible that this represents an early stage in the development of a rudimentary Juel's organ.

It should be pointed out that a uterine seminal receptacle was not present in our sectioned material, and its presence or absence could not be ascertained either from the literature or from whole-mounts. Considering that there is no alternative seminal storage apparatus and that it is present in *Prosorchis*, we can only assume that it is normally present in *Prosorchiopsis*.

Addendum to Sclerodistomidae

It is possible that *Eurycoelum* Brock, 1886, and *Distoma gigas* Nardo, 1827, two forms not recorded since the nineteenth century, are also sclerodistomids; but the descriptions of these taxa are incomplete. *Eurycoelum sluiteri* was described (Brock, 1886) from the stomach of *Lutjanus sanguineus* [= *Diacope metallicus*] off Java. The genus has been considered by certain workers, including Yamaguti (1971), to be a synonym of *Hemiurus*; but this is not the case. In fact it is possible that this genus may be a synonym of *Prosogonotrema*, which has been recorded from *Lutjanus* spp. on several occasions; but only an examination of the type-specimens, which

we have been unable to trace, or material from the type-host and locality can substantiate this. The situation with regard to *Distoma gigas*, a gigantic species from the stomach of *Luvarus imperialis*, has been discussed in detail by Gibson & Bray (1977).

SCLERODISTOMOIDIDAE fam. nov.

Body large; stout, elongate oval and attenuated anteriorly. Ecsoma absent. Body-surface smooth. Oral and ventral suckers well developed, small; ventral sucker well inside anterior half of body. Prepharynx absent. Pharynx well developed. Oesophagus short. 'Drüsenmagen' present. Gut-caeca sinuous; end blindly near posterior extremity, very close to stem of excretory vesicle (no union observed). Testes two; slightly lobate; symmetrical to oblique; in hindbody close to ventral sucker; pre-ovarian. Seminal vesicle tubular convoluted in forebody. Pars prostatica short; tubular with wide lumen. Ejaculatory duct short. Hermaphroditic duct short; present within small, cone-shaped permanent sinus-organ. Sinus-sac small and poorly developed or apparently absent. Genital atrium well developed. Genital pore mid-ventral at level of pharynx. Ovary oval; in middle of body; separated from testes by loops of uterus. Mehlis' gland postero-lateral to ovary. Laurer's canal and uterine seminal receptacle present. Canalicular or blind seminal receptacle and Juel's organ absent. Uterus inter-caecal; coiled almost entirely in hindbody, in both pre- and post-ovarian fields; with narrow, convoluted descending loop reaching near to posterior extremity and convoluted ascending loop which is initially narrow and then much broader. Eggs small; numerous; without filaments. Vitellarium tubular; with two main collecting ducts situated medially, one anteriorly and other posteriorly oriented; laterally directed dendritic branches present between testes and level a short distance anterior to posterior extremity. Excretory vesicle Y-shaped; stem short; arms initially in dorsal and ventral fields, pass laterally and unite in forebody. Parasitic in gall-bladder of marine teleosts.

COMMENT. We have erected a new family for the genus *Sclerodistomoides* Kamegai, 1971, because it differs significantly from the accacoeliids in the structure of the pharynx, from the sclerodisto-mids in the absence of Manter's organ, and from both groups in the unique orientation of the main collecting ducts of the vitelline system. Its closest relative appears to be the accacoeliid genus *Paraccacladium*.

SCLERODISTOMOIDES Kamegai, 1971   [T(w); t(s)]

Defined as family.

TYPE-SPECIES. *Sclerodistomoides pacificus* Kamegai, 1971 [by original designation].

COMMENT. *Lintonius novikovi* Baeva, 1965, does bear some superficial resemblance to *Sclerodistomoides*, but the description of this species by Baeva (1965) does not include enough data to confirm this. Yamaguti (1971) suggested that it might be a sclerodistomid.

Family SYNCOELIIDAE Looss, 1899

Body elongate or dorso-ventrally flattened; usually with pedunculate ventral sucker. Ecsoma absent. Body-surface smooth, but commonly papillate on forebody and on peduncle, if present. Oral and ventral suckers well developed; may possess accessory suckers around their rim. Glandular cells common in subtegumentary parenchyma and within musculature of suckers. Pharynx well developed. Oesophagus short. Cyclocoel usually present, but gut-caeca may end blindly (?) or form a uroproct. Testes eleven to eighteen distinct, oval follicles (usually arranged in pairs), seven to eight transverse rows of small follicles, or just a large number of irregular follicles; pre-ovarian, in hindbody. Seminal vesicle thin-walled; tubular; winding or sinuous; in forebody. Pars prostatica tubular. Ejaculatory duct short. Hermaphroditic duct and genital atrium present, but indistinguishable when sinus-organ is absent. Permanent sinus-organ and sinus-sac present or absent. Genital pore mid-ventral in anterior forebody. Ovary post-testicular; composed of five large, oval, isolated lobes or numerous irregular follicles. Laurer's canal and

uterine seminal receptacle present. Juel's organ and canalicular or blind seminal receptacle absent, but rudimentary seminal receptacle may be present. Uterus passes posteriorly but coils mainly in pre-ovarian hindbody. Eggs numerous, small, non-filamented. Vitellarium usually seven (occasionally five or six) isolated, oval lobes, or irregular acinous bunches or rows of follicles; post-ovarian. Excretory vesicle Y-shaped; arms united in forebody, may initially run in dorsal and ventral fields. Free floating metacercarial stage present. Parasitic in branchial and buccal cavities, on skin, in (?) oviduct and in (?) gut of elasmobranchs and marine teleosts.

Key to Syncoeliidae

1. A. Ovary numerous irregular follicles arranged in rows; vitellarium irregular acinous
        bunches or rows of follicles   .   .   .   .   .   **OTIOTREMATINAE** (p. 115)
   B. Ovary 5 large isolated lobes; vitellarium 5 to 7 oval, isolated lobes .   **SYNCOELIINAE** (p. 116)

Subfamily **SYNCOELIINAE** Looss, 1899

Small accessory suckers around rim of suckers absent. Peduncle usually present. Cyclocoel present. Testes eleven to eighteen distinct, oval lobes; usually arranged in pairs. Permanent sinus-organ present or absent. Hermaphroditic duct and genital atrium present, but indistinguishable when sinus-organ is absent. Sinus-sac absent or rudimentary. Ovary composed of five large, isolated follicles. Rudimentary seminal receptacle may be present as proximal dilation of Laurer's canal. Uterus arranged in large, regular loops dorsally and ventrally to gonads. Vitellarium seven (occasionally five or six) small, isolated, oval lobes. Parasitic in branchial and buccal cavities (? with occasional records from gut) of sharks and marine teleosts.

COMMENT. Our work with this group indicates that *Syncoelium* Looss, 1899, can be conveniently split into two distinct genera on the basis of the presence or absence of a sinus-organ (Gibson & Bray, 1977). When present, the sinus-organ is a well-developed structure, visible in sections and whole-mounts in both adults and metacercariae (see Gibson, 1976). In addition, in forms lacking a sinus-organ the genital atrium appears to be indistinguishable from the hermaphroditic duct, the hindbody tends to be spatulate rather than tubular, and the ventral sucker is somewhat less pedunculate. Furthermore, the latter forms have been recorded from the gills, whereas the forms possessing a sinus-organ usually occur in the buccal cavity and on the gill-arches.

Key to Syncoeliinae

1. A. Permanent sinus-organ absent; hermaphroditic duct indistinguishable from genital atrium;
        tendency for hindbody to be spatulate; ventral sucker normally sessile or on short
        peduncle; normally parasitic on gills   .   .   .   .   .   .   *SYNCOELIUM*
   B. Permanent sinus-organ present; hermaphroditic duct easily distinguishable from genital
        atrium; hindbody usually tubular; ventral sucker usually on well-developed peduncle;
        usually parasitic in buccal cavity or on gill-arches   .   .   .   .   *COPIATESTES*

SYNCOELIUM Looss, 1899

Hindbody broad or spatulate. Ventral sucker sessile or surmounted on short peduncle. Permanent sinus-organ absent. Hermaphroditic duct indistinguishable from genital atrium. Parasitic on gills (? and in intestine) of sharks and marine teleosts.

TYPE-SPECIES. *Syncoelium ragazzii* (Setti, 1897) [by monotypy].

*COPIATESTES** Crowcroft, 1948   [n(w,s)]

Hindbody elongate, tubular. Ventral sucker surmounted on well-developed peduncle. Permanent sinus-organ present. Hermaphroditic duct and genital atrium easily distinguishable. Parasitic in

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* It is also spelt *Capiatestes* in original publication, but this is a typographical error.

branchial (especially gill-arches and gill-rakers) and buccal cavities (? and intestine) of marine teleosts.

TYPE-SPECIES. *Copiatestes thyrsitae* Crowcroft, 1948 [by original designation].

Subfamily OTIOTREMATINAE Skrjabin & Guschanskaja, 1957

Paronatrematinae Skrjabin & Guschanskaja, 1957 [proposed, but not named, by Dollfus (1950)].

[*Paronatrema* is poorly known.] Accessory suckers may be present around rim of suckers. Cyclocoel present (? or absent; caeca may end blindly or form uroproct). Testes numerous irregular follicles or seven to eight irregular transverse rows of follicles. Hermaphroditic duct present within sinus-sac (? not clearly described in *Paronatrema*). Permanent sinus-organ absent. Ovary composed of numerous irregular follicles which may be arranged in rows. Vitellarium irregular acinous bunches or rows of follicles. Parasitic in branchial cavity or on skin (? or in oviduct or intestine) of sharks and rays.

Key to Otiotrematinae

1. A. Small accessory suckers present on oral sucker and/or ventral sucker . ***PARONATREMA***
   B. Small accessory suckers on suckers absent (papillae present within oral sucker) ***OTIOTREMA***

OTIOTREMA Setti, 1897   [t(w,s)]

Forebody cylindrical; hindbody flattened, alate, recurved. Papillae present within oral sucker; small accessory suckers within suckers absent; ventral sucker pedunculate. Gut-caeca sinuous in forebody; with numerous diverticulate outgrowths in hindbody; forming cyclocoel. Sinus-sac large, reaching close to dorsal surface. Ovary and vitellarium consisting of numerous acinous bunches of follicles, posterior to numerous follicular testes. Uterus in transverse coils; present in lateral fields of hindbody. Parasitic in branchial cavity (? or intestine) of sharks.

TYPE-SPECIES. *Otiotrema torosum* Setti, 1897 [by original designation].

COMMENT. We have examined some of the material collected by Looss, and it appears to agree well with his description (Looss, 1899).

PARONATREMA Dollfus, 1937   [t(w); n(w)]

[This genus is poorly known.] Forebody sub-cylindrical; hindbody flattened, oval. Small accessory suckers present within oral and/or ventral suckers; ventral sucker large, but apparently not pedunculate. Gut-caeca sinuous; apparently end blindly (? or form uroproct or cyclocoel: interpretations uncertain). Testes consist of rows of follicles or segmented tubules. Ovary composed of irregular follicles (interpretations conflict). Vitellarium consists of rows of follicles or segmented tubules. Uterus numerous transverse coils in hindbody. Parasitic on skin or (?) in oviduct or stomach of sharks and rays.

TYPE-SPECIES. *Paronatrema vaginicola* Dollfus, 1937 [by monotypy].

COMMENT. It would appear that in some descriptions the ovary and Mehlis' gland may have been confused.

Generic Index to part III

IV. A discussion on the evolution of the Hemiuroidea

Evolutionary trends in the Hemiuroidea

The presentation of any evolutionary picture for the Platyhelminthes must remain hypothetical, as it is unlikely that there will ever be any fossil record due to the soft-bodied nature of these animals. Possible evolutionary patterns can only be exposed by the knitting together of general morphological trends in organs, organ-systems and whole animals. Having distinguished a trend, there is the problem of deciding which way the trend is moving, and hence which is the primitive and which is the advanced condition. In addition, the possibility should not be forgotten that an intermediate form is primitive and that evolution is proceeding in two opposite directions. In order to assess which form is primitive, it is helpful to adopt the use of certain external indicators. As far as parasitic helminths are concerned useful indicators include:

1. *The supposed 'primitiveness' of the host*
   Although superficially it appears more likely that the more archaic and primitive vertebrates harbour more archaic and primitive parasites, this is not necessarily so. Owing to the variable

ecological factors involved, archaic hosts can harbour what appear to be 'advanced' parasites, and *vice versa*. In addition, there are often widely differing opinions as to the relative ages of certain groups of vertebrates, and this tends to limit its value as an indicator. One might expect, however, that a group of helminths restricted to birds would be more advanced than one restricted to elasmobranchs. Unfortunately, the vast majority of the hemiuroids are parasitic in fishes, and, although certain primitive groups are recognized, it is not known for certain whether elasmobranchs are more primitive than bony fishes (Osteichthyes).

Amongst the hemiuroids only the azygiids appear to occur in fishes which are widely held to be primitive. *Otodistomum* commonly occurs in the shark *Hexanchus* and has been recorded from *Chlamydoselachus* and *Heterodontus*, and both *Azygia* and *Leuceruthrus* occur in the holostean *Amia*. Other groups occuring in elasmobranchs are the ptychogonimids and the syncoeliids, the Ptychogonimidae and the Otiotrematinae being entirely restricted to these hosts. *Azygia* has also been recorded from *Acipenser*, a member of primitive group Chondrostei; but little emphasis can be placed upon this result as *Derogenes* and several species of hemiurid have also been recorded from this host. This apparent mixture of what we believe to be 'primitive' and relatively 'advanced' forms is possibly associated with the migratory habit of sturgeons and the low degree of host-specificity exhibited by some of the more 'advanced' hemiuroids. There is also a single record of *Halipegus* from the related chondrostean *Polyodon*. Except for certain halipegine derogenids, which occur in amphibians and, rarely, in amphibious snakes, and the pulmovermine hemiurids, which are restricted to the lungs of sea-snakes, the remainder of the hemiuroids occur in teleosts.

2. *The habitat of the host*
   Parasites of aquatic vertebrates will tend to be more primitive than those from terrestrial vertebrates, because aquatic vertebrates tend to be more primitive than terrestrial vertebrates and because it is much easier to envisage the origins of parasitic platyhelminths in aquatic conditions. All the hemiuroids are parasitic in aquatic or amphibious hosts, the majority being parasitic in marine teleosts, but a few groups are commonly found in freshwater hosts. Unfortunately, there is no conclusive evidence to suggest that teleosts arose in freshwater, or *vice versa*, although a freshwater origin is preferred by some workers. It should be emphasized that any evidence based upon the habitat of the host should be treated with caution, as various hosts may have passed from fresh- to salt-water or from water to land, and back, on more than one occasion during the course of their evolution.

Amongst the hemiuroids, only the azygiids and the halipegine derogenids are successful parasites of freshwater fishes, and only the isoparorchiids, a very small group, are restricted to these hosts. One interesting coincidence is that all three of the azygiid genera from freshwater fishes occur in North America, two being endemic, and that this is the only region of the world where holostean fishes survive. Another possible coincidence is that the majority of halipegine genera and the majority of isoparorchiid records occur in Asia, especially in the southern half of the continent: this location is the possible centre of evolution and radial dispersion of freshwater teleosts (see Darlington, 1957).

3. *Host-specificity*
   One might expect helminths with a high-degree of host-specificity to be more primitive than those with a low-degree. This is because it is likely that highly specific associations develop over a long period of time, and once they have arisen the further evolution of the parasite itself tends to be restricted to within the limits of the evolution of the host. This is a very general feature, however, and as digeneans tend to have a low degree of host-specificity with regard to their vertebrate host, it is of limited value.

It is worth noting, nevertheless, that the host-range of the adult forms of certain groups and genera do tend to be restricted. The accacoeliines, with the exception of *Tetrochetus*, occur only in molid teleosts and the ptychogonimids appear to be entirely or almost entirely restricted to galeomorph sharks. *Bathycotyle* and *Hirudinella* parasitize scombroid and coryphaenid teleosts,

and *Botulus* and *Lampritrema* are usually restricted to *Alepisaurus* and *Lampris*, respectively. Prominent among other examples are the macradeninine and quadrifoliovariine lecithasterids, which occur only in acanthurid teleosts. Alternatively, many members of the Hemiuridae, Lecithasteridae, Bunocotylidae and Derogenidae appear to exhibit little or no host specificity amongst marine teleosts, although certain individual species or genera may appear to be highly host-specific. One species of *Halipegus* is reported to occur in freshwater teleosts and amphibians. The azygiids are present in freshwater teleosts, elasmobranchs, holosteans and rarely in chondrosteans, and although they appear to be restricted to certain groups of elasmobranchs, they appear to exhibit little host-specificity.

It is obvious in many of the above cases, e.g. the accacoeliines, that much of the apparent host-specificity is ecological rather than immunological or physiological, and it is likely that ecologically based host-specificity has less evolutionary significance, as it would appear that an ecological restriction is a prerequisite for the development of other types of host-specificity. Our lack of knowledge of the life-history in many cases, however, prohibits the differentiation of these types. Nevertheless, the above examples do tend to illustrate the fact that there is a tendency for the successful groups, such as derogenids, hemiurids, lecithasterids and bunocotylids to exhibit in general a low degree of host-specificity, while the smaller groups, such as accacoeliids, hirudinellids, ptychogonimids, etc. tend to be more restricted. If our hypothesis that host-specificity is acquired over a long period of association is correct, then it is likely that these smaller groups will tend to be more primitive than the larger. The azygiids occupy an anomalous position in that to some extent they are restricted to particular groups of fishes, but within these groups they are widespread. This might be explained by the fact that they are a small, but successful, group which occupy niches, i.e. the stomach of freshwater fishes and elasmobranchs, where competition from other digeneans is severely limited.

4. *Related groups*

Undoubtedly the most important evidence can be taken from features common in groups which are held to be related to, and perhaps more primitive than, the group under study. Digeneans, monogeneans, cestodes and aspidogastreans are generally thought to have evolved from primitive rhabdocoel turbellarians, possibly similar to the Dalyellida, which may inhabit the mantle-cavity or viscera of bivalves. Most authorities now agree that the Aspidogastrea is the closest relative of the Digenea, and Rohde (1971a) in an abstract states: 'The Aspidogastrea are considered to be primitive, direct decendents of turbellarians, which are not yet closely adapted to parasitism and have not yet incorporated the vertebrate host as a fixed component in their life-cycle. They are closely related to the ancestors of the Digenea. Aspidogastrea and Digenea are both primarily parasites of molluscs.' In the same context Rohde (1971b) refers to the Aspidogastrea as 'living fossils'. It is likely, therefore, that features common to the Aspidogastrea and Digenea either must be primitive or are features produced by parallel or convergent evolution. Some primitive features may also be common in other parasitic platyhelminths and in the rhabdocoels; but, since these groups are successful, widely specialized and more distantly related, great care should be taken in the interpretation of any correlations, as the same features have undoubtedly been evolved independently by parallel and convergent evolution. Beklemishev (1964 [1969]), for example, states, when discussing the reproductive system of the Platyhelminthes: 'In spite of the great diversity of these adaptations, which appear independently in the various groups, the problems involved are repeatedly solved by similar methods, and that in animals far apart in the system.'

When attempting to decide which of a group is primitive, one must, therefore, look for a succession of trends which tend to flow in the same direction. It is unlikely, however, that one will encounter all of the trends proceeding 'satisfactorily' in the same animal. It is a fact that parallel and convergent evolution do occur, and each species is adapted to its particular niche rather than to illustrate an evolutionary picture. Parallel evolution is important because, as the members of the group originally shared the same gene-pool, the same mutations are likely to occur down the separate evolutionary branches, and thus the same features may evolve independently in several

different sub-groups. It is essential, therefore, that one looks at the overall trends in the group as a whole. This is especially important where the loss of organs may have occurred.

In an attempt to show the evolutionary trends within the Hemiuroidea, we have followed three different organs and organ-systems in which definite trends do occur. These are: (1) the seminal storage and disposal apparatus in the female reproductive system; (2) the vitellarium; and (3) the terminal genitalia.

(1) *Seminal storage and disposal apparatus in the female reproductive system*. One of the most significant, but not one of the most obvious, trends in the Hemiuroidea is the development of the seminal storage and disposal apparatus, especially the latter, in the female system. In the majority of hemiuroids the proximal region of the uterus forms a seminal reservoir and is termed the *uterine seminal receptacle*. As a uterine seminal receptacle occurs in the Aspidogastrea (see Rohde, 1971a), it is likely that this condition is primitive in digeneans. Evidence from other platyhelminth-groups is difficult to interpret as they are specialized and involve, in the case of the Turbellaria, a vagina (copulatory canal) and several different types of seminal receptacle, and, in the case of the Monogenea and Cestoda, usually a vagina (or vaginae) with a dilation which forms a seminal receptacle. However, in some rhabdocoel turbellarians such as *Mesostoma*, a seminal receptacle in the form of a dilation of the oviduct does occur. Considering that the ovo-vitelline canal, which is the equivalent of the uterus in the Digenea, is short and that there is no Mehlis' gland, this feature is somewhat similar to a uterine seminal receptacle.

As stated above, the sperm in the majority of hemiuroids is stored in the proximal region of the uterus. From the uterus small amounts of activated sperm pass through Mehlis' gland, where presumably fertilization of the ova usually occurs. Excess and spent sperm, plus excess vitelline material, are then disposed of via Laurer's canal, which in certain groups, e.g. the Azygiidae, Accacoeliidae and Hirudinellidae, connects the oviduct with the exterior via a dorsal pore (see Fig. 6; arrangement A). Such sperm and vitelline material in Laurer's canal can be seen in sectioned material: occasionally ova are also present. This process is naturally very wasteful, and it is apparent that certain turbellarians and monogeneans have developed an analogous duct, the genito-intestinal canal, which disposes of similar residues by transporting them into the gut, in order that this material can be re-processed. Our work has shown that some hemiuroids appear to have evolved a special organ, *Juel's organ*, within which this waste-material is degraded and re-absorbed. It is clear that this organ did not arise overnight, as traces of its development can be seen in present forms. In groups, such as Gonocercinae, Syncoeliinae and Isoparorchiidae, the proximal region of Laurer's canal is slightly dilated, forming a *rudimentary seminal receptacle*, within which excess spermatozoa and vitelline material are stored before passing along the remainder of the canal (see Fig. 6; arrangement B). Our observations suggest that the excess material is killed or stored until it dies, and that it may begin to disintegrate within the rudimentary seminal receptacle, before being passed along the canal. The distal part of the canal in these groups tends to be slightly glandular in nature, and the pore itself is often tightly closed by a sphincter: thus, it is possible that some re-absorption may occur in these distal regions. In forms such as *Derogenes* and apparently *Prosorchis*, a *rudimentary Juel's organ* is found (see Fig. 6; arrangement C). In these cases the Laurer's canal does not open to the exterior, as the distal part of the duct is modified and forms an oval structure with a similar amorphous appearance to that of a fully-developed Juel's organ. During the course of evolution, Laurer's canal has become shorter, thus bringing the rudimentary Juel's organ and rudimentary seminal receptacle closer together. In *Prosogonotrema* these two structures are very close together (Fig. 4B). This process has continued until the rudimentary Juel's organ completely envelopes the rudimentary seminal receptacle, thus forming a complete Juel's organ (see Fig. 6; arrangement D). The enclosed rudimentary seminal receptacle has been known in the past as the 'inner vesicle' (Juel, 1889; Lander, 1904). A complete Juel's organ has been observed in *Genarchopsis* (Anjaneyulu, 1968; Madhavi & Rao, 1974), *Elongoparorchis* (Madhavi & Rao, 1974), in numerous hemiurids, knowingly or unknowingly, by several authors, including Juel (1889) and Lander (1904), and by ourselves in various hemiurids, *Hysterolecitha* and *Arnola*. A final development, which appears to have occurred during the development of the Opisthadeninae, and
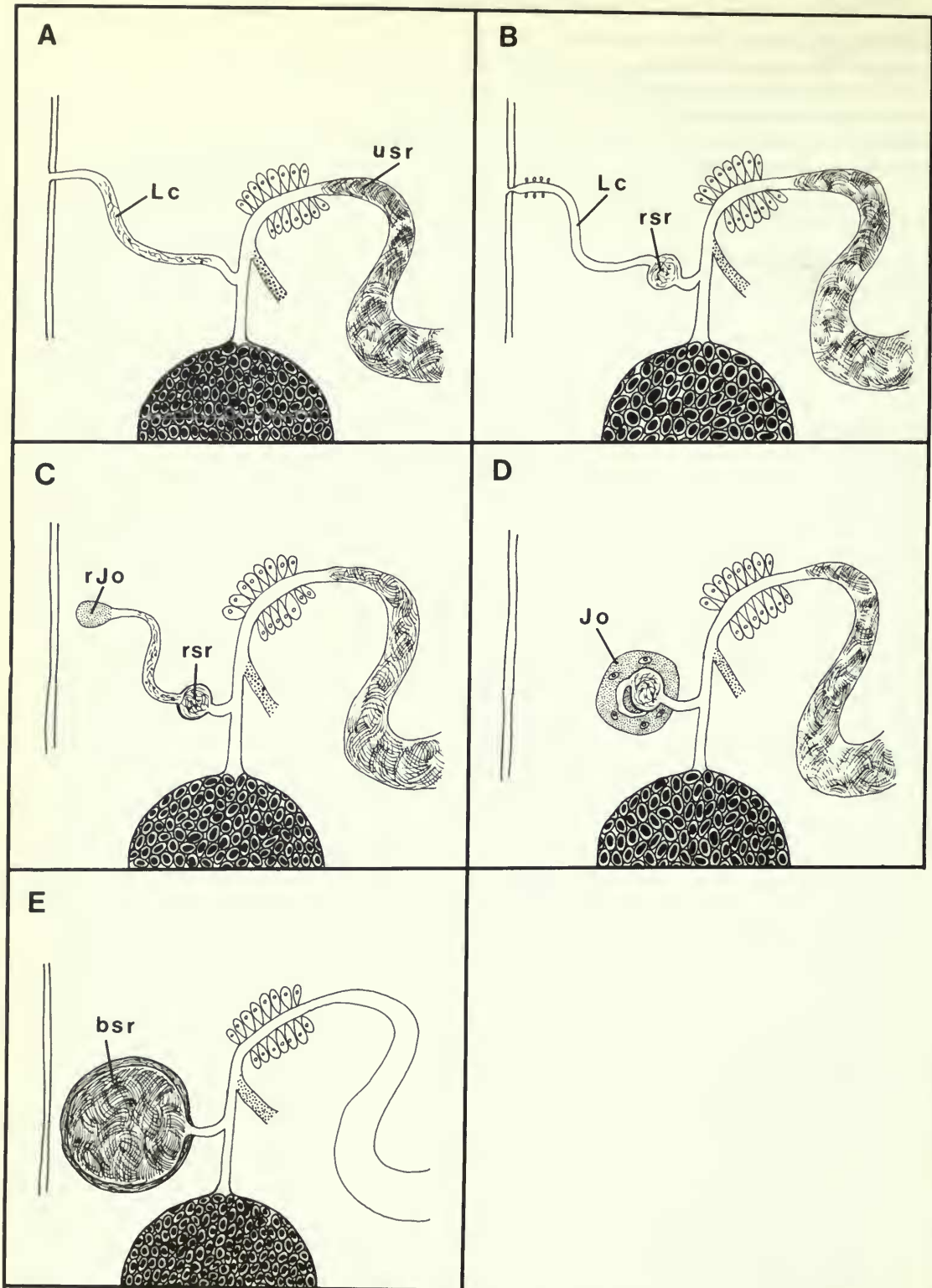
Fig. 6 Different arrangements of the seminal storage and disposal apparatus in the female reproductive system (see text). [bsr, blind seminal receptacle; Jo, Juel's organ; Lc, Laurer's canal; rJo, rudimentary Juel's organ; rsr, rudimentary seminal receptacle; usr, uterine seminal receptacle.]

probably the majority of the lecithasterids, is that the inner vesicle expands to fill Juel's organ, thus forming a *blind seminal receptacle* (see Fig. 6; arrangement E). The uterine seminal receptacle is lost in these groups. A blind seminal receptacle tends to be a large, thick-walled structure, which is connected to the oviduct by a narrow duct: the sole remnant of the original Laurer's canal. This final development presumably means that the spermatozoa pass through Mehlis' gland in the opposite direction to that which normally occurs in the remainder of the hemiuroids. Spent spermatozoa and excess vitelline material are, therefore, voided via, or broken down and re-absorbed by, the uterus.

The evidence, which suggests that the presence of Laurer's canal opening to the exterior in conjunction with a uterine seminal receptacle is primitive, is that this is exactly the same arrangement which occurs in the majority of aspidogastreans (e.g. *Multicotyle, Lophotaspis, Cotylogasteroides, Macraspis*). The development of a seminal and vitelline disposal organ, however, is not limited to the Juel's organ of some hemiuroids. It appears that analogous structures may have developed in an aspidogastrean and certain turbellarians. Stafford (1896) described Laurer's canal of *Aspidogaster conchicola* Baer, 1826, as ending blindly in the form of a 'thick-walled bulb', and Voeltzkow (1888) refers to the same structure as a 'receptaculum vitelli' because it appeared to contain vitelline residues.* The absorption of excess sperm by the Turbellaria is discussed by de Beauchamp (1961, p. 31). He notes that, in addition to the genito-intestinal canal which occurs in some groups, there appear to be several different organs involved: these include the 'vesicle of Lang' of the polyclads (see Bock, 1927), the 'vesicula resorbiens' of the Kalyptorhynchia, and the copulatory bursa, which is found in many turbellarians. It is clear that, while there is a need to dispose of excess and spent seminal and vitelline material, there is in free-living helminths a strong selective pressure for the development of an organ of re-absorption, which thus aids the animal's economy. Owing to the ready availability of food, this pressure is probably much less in the parasitic forms, as demonstrated by the number of digeneans which still use Laurer's canal as a seminal and vitelline drain, but it would still appear to be advantageous to the economy of the parasite for it to develop a less wasteful system. If the actual biology of these digeneans is examined in detail, it is clear that many hemiuroids are stomach-parasites, and that they have developed mechanisms which protect them from the low pH and, in the case of marine teleosts, the high osmolarity of the environment (MacKenzie & Gibson, 1970; Gibson, 1971). The hemiurids which live in such conditions apparently withdraw their ecsoma and contract, with the result that they are protected by their thick tegument, and the derogenids from the stomach tend to migrate anteriorly towards the oesophagus during periods of low pH or high osmolarity. These parasites, therefore, contrary to intestinal forms, do not appear to be in a position to feed at all times. It would seem, consequently, that it is advantageous for these parasites to re-utilize some of its waste-material in order to help maintain egg-production during periods when feeding is limited.

The presence of a structure resembling a rudimentary Juel's organ in *Aspidogaster conchicola* does suggest that Juel's organ may also be a primitive feature; but this structure appears not to have been observed in other aspidogastreans. In addition, it appears that a similar structure may be present in digeneans unrelated to the hemiuroids, e.g. *Styphlodora bascaniensis* Goldberger, 1911 (see Goldberger, 1911b), and *Cyclocoelum sharadi* Bhalerao, 1935 (see Madhavi & Rao, 1974), and that this feature has not apparently been reported in other species of these genera which have been examined. It would seem, therefore, that a distal modification of Laurer's canal, which appears to be associated with the degradation of seminal and vitelline material, has been independently evolved on at least four different occasions. This would appear to vindicate Beklemishev's statement quoted above. Only in the hemiuroids, however, does this organ appear to have developed further, i.e. past the 'rudimentary' stage, and only in the hemiuroids is it common to entire groups. In other instances, it appears to have been developed independently by

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* Voeltzkow claimed to have seen the canal open to the exterior in young animals, and that the 'receptacle' developed as the animal matured. Stafford, however, was of the opinion that Laurer's canal developed as an outgrowth from the oviduct.

species, possibly recently, to meet their present ecological requirements. This is supported by the fact that none of the latter species are gut-parasites, and, therefore, such a development would probably be economically advantageous.

Many digeneans have lost Laurer's canal, or have altered its function, i.e. in some groups it is used as a vagina. The latter occurrence we consider to be an advanced feature (Gibson & Bray, 1975), and species which use this method of copulation (one sided, as opposed to the possibility of reciprocal copulation where the genital atrium is used) normally have a thin-walled *canalicular seminal receptacle*, formed as a proximal dilation of Laurer's canal, and no uterine seminal receptacle, e.g. *Diphterostomum brusinae* (Stossich, 1889) and *Haploporus benedeni* (Stossich, 1887) – see Palombi (1931). We should emphasize that remarkably few digeneans have ever been seen in the act of copulation.

Assuming, from the above evidence, that the presence of Laurer's canal opening dorsally and a uterine seminal receptacle are, in the Hemiuroidea, primitive characters, it is not unreasonable to presume that Juel's organ has evolved in the manner described above. The derivation of the blind seminal receptacle of the opisthadenines and the majority of the lecithasterids from Juel's organ is not so obvious. If one discounts the possibility that it arose independently as a diverticulum of the oviduct, there appears to be only one other alternative. That is, its independent derivation from the rudimentary seminal receptacle. In the Lecithasteridae, *Trifoliovarium* has a large, functional canalicular seminal receptacle which has presumably evolved directly from a rudimentary seminal receptacle. The blind seminal receptacle of the related *Cladolecithotrema* has presumably evolved by the loss of Laurer's canal. Alternatively, in *Hysterolecitha* and presumably *Hysterolecithoides* Juel's organ is present. The blind seminal receptacle of the remainder of the lecithasterids could, therefore, have evolved from either a rudimentary seminal receptacle or Juel's organ. As the inner vesicle of Juel's organ appears to have been derived from the rudimentary seminal receptacle, this is essentially the same thing; but the thick, fibrous wall of the blind seminal receptacle is quite different to the relatively thin-walled type of seminal receptacle which usually occurs in digeneans. This suggests that the wall of the blind seminal receptacle may be derived from the outer capsule of Juel's organ. There is also evidence that the blind seminal receptacle of the opisthadenines has evolved from Juel's organ of the hemiurids and, as discussed below, that a similar blind seminal receptacle appears to have arisen independently from Juel's organ in the Didymozooidea.

Although the form of the seminal storage and disposal system tends to be relatively constant within a family or subfamily, there is a notable exception to this. In the Derogenidae a variety of conditions occur: (1) many halipegines, such as *Halipegus*, possess Laurer's canal, which opens dorsally, and a uterine seminal receptacle; (2) other forms, such as the Gonocercinae, are similar except that a small, but distinct, rudimentary seminal receptacle occurs; (3) in the remainder of the halipegines, such as *Genarchopsis* [but see p. 79] and *Arnola*, a fully developed Juel's organ is present; and (4) in the derogenines a continuous variation of conditions occur: (a) *Derogenes* possesses a large rudimentary seminal receptacle containing spermatozoa which is connected by Laurer's canal to a rudimentary Juel's organ; (b) in *Progonus* the rudimentary seminal receptacle is further enlarged to function as the only seminal store, the uterine seminal receptacle being lost, and the rudimentary Juel's organ is present at the junction of the seminal receptacle and Laurer's canal, which ends blindly; and (c) in *Leurodera* Laurer's canal and the rudimentary seminal receptacle appear to have been lost, leaving a blind seminal receptacle. The variation which occurs in this group can perhaps be explained by the fact that it is a large, successful group, possibly with primitive origins, arising at about the time when the first variations of the primitive seminal storage and disposal apparatus, such as the development of Juel's organ, were beginning to occur. It is possible that parallel evolution is responsible for some of the conditions which occur in this group and their apparent similarity to the arrangements in other hemiuroid groups.

(2) *Vitellarium.* There appears to be a very clear trend in the form of the vitellarium in the Hemiuroidea. Briefly, commencing with a follicular form, and passing through tubular and seven-lobed stages, the vitellarium is finally reduced to two, or occasionally one, oval masses. The trend begins with the follicular vitellarium which occurs in the Azygiidae (Fig. 7; arrangement A).
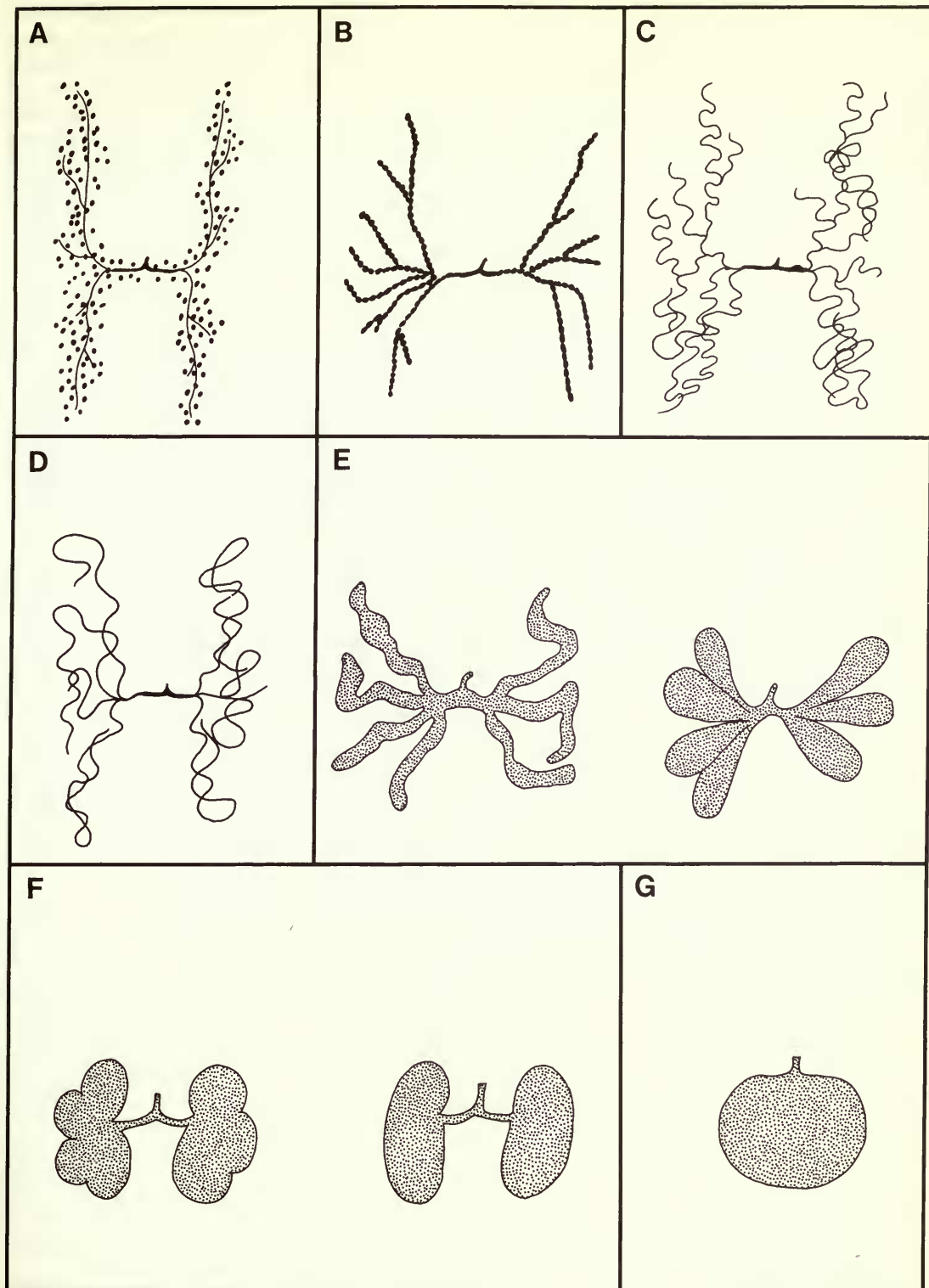
Fig. 7 Different arrangements of the vitellarium (see text).

These follicles become linked together along the collecting ducts, thus giving a chain-like appearance, as occurs in the syncoeliid *Otiotrema* and to some extent in the accacoeliid *Tetrochetus* (Fig. 7; arrangement B). The vitellarium then becomes distinctly tubular, consisting of many long, often convoluted, tubules, which may be branched (Fig. 7; arrangement C). The latter type of vitellarium occurs in the Accacoeliidae, Hirudinellidae and Isoparorchiidae. The next stage is that the number of tubules, which are usually unbranched, is reduced to seven: these usually being arranged with three on one side of the body and four on the other (Fig. 7; arrangement D); e.g. some sclerodistomids and some hemiurids, such as *Dinurus* and *Stomachicola*. The length of the seven tubules is then gradually reduced, so that they pass through digitiform (e.g. *Lecithocladium*, *Plerurus*, *Ectenurus*), tear-shaped (e.g. *Elytrophallus*, *Lecithaster*, *Hysterolecitha*) and oval (*Prolecitha*, *Dichadena*, *Lecithophyllum*, *Syncoelium*) stages (Fig. 7; arrangement E). The seven lobes, whether tubular, digitiform, tear-shaped or oval, may form a rosette arrangement, with three lobes on one side and four on the other, or may form two separate groups of three and four lobes which are connected by the collecting ducts. Presumably from the latter arrangement have developed forms, such as *Dinosoma* and *Arnola*, with two vitelline masses which are distinctly three- and four-lobed (Fig. 7; arrangement F). The lobation then tends to be almost or entirely lost (e.g. *Hemiurus*, *Brachyphallus*), resulting in forms, such as *Derogenes*, *Lethadena* and *Myosaccium*, with two totally unlobed, oval masses. In genera such as *Bunocotyle*, *Monolecithotrema*, *Monovitella* and *Chenia* the vitellarium is present as a single entire or slightly lobed mass (Fig. 7; arrangement G). This mass was probably, and almost certainly in the latter two cases, formed from the fusion of two oval masses; but there is a possibility that it could be the result of either the loss of one mass or the condensation of a rosette-arrangement.

It must be emphasized here that the above is only a general trend in the form of the vitellarium, as there is a certain amount of variation within each group, particularly within the hemiurids and the lecithasterids. For example, a relatively common feature of the lecithasterids is a doubling of the number of vitelline lobes. In addition, the number of vitelline tubules or lobes, commonly seven in many of the hemiuroids, is variable, six, eight or nine frequently being reported. The presence of nine (four and five) lobes is especially common on the two vitelline masses of the halipegine derogenids.

As the various links in the above pattern do appear to illustrate the trend relatively clearly, the only real problem is to find evidence which indicates that the follicular arrangement of the vitellarium is primitive. It appears, however, that a follicular vitellarium is found in the majority of monogenean and cestode groups, in all aspidogastreans and also in some rhabdocoel turbellarians, e.g. *Mesostoma*. This suggests very strongly that the follicular arrangement is primitive. It is likely that the duplication of the vitelline glands, resulting in the follicular arrangement, occurred as an early development to accommodate an increase in egg-production. This would have been especially necessary when the 'ancestral rhabdocoel' became an obligate parasite. This is emphasized by evidence from the digenean *Schistosoma mansoni* Sambon, 1907, which indicates that thirty to forty vitelline cells are present in each egg (Gönnert, 1955). The widespread spacial arrangement of this highly metabolically active organ-system in the 'primitive' forms is probably a mechanism to aid the absorbtion of nutrients from the surrounding parenchymatous tissue, rather like the roots of a tree. Even though food is often continually available to the 'primitive' hemiuroids, such as the azygiids and hirudinellids, they tend to be rather large for digeneans, and, therefore, still have certain problems with regard to the diffusion of nutrients. The more 'advanced' hemiuroids tend to be smaller in size, and, therefore, there is no longer such a need for a widespread follicular, dendritic or simple tubular vitelline system, as the problems associated with the diffusion of nutrients are reduced. In addition, there is more competition for space, as the uterus tends to take up a much greater proportion of the body. This latter factor, plus the economic advantage in reducing the distance involved in the transportation of vitelline material, adequately explains the reduction of the vitellarium to a small rosette or to one or two masses.

One apparent contradiction is the vitelline structure of the syncoeliine syncoeliids, which, as it consists of seven oval lobes, indicates that it is far more 'advanced' than the remainder of the

anatomy. The premature reduction in the size of the vitellarium can be explained, however, by certain modifications in the process of egg-formation which appear to occur in this group. Our observations suggest that the eggs of *Copiatestes* are produced in a uterine oötype (see glossary), have a membranous 'shell' and contain only one, or a very small number, of vitelline cells. During the egg's passage down the uterus the vitelline cell(s) appear to replicate many times, the membranous 'shell' permitting the diffusion of nutrients into the egg as a source of material and energy for this process. Not until a full complement of vitelline cells is present, at about the middle of the uterus, does the egg-shell become thicker, tanned and hardened. The demand on the vitellarium for vitelline cells appears, therefore, to be greatly reduced, possibly by a factor of twenty to thirty times. Some aspects of egg-shell formation have been described by Gibson (1976) for *Copiatestes filiferus* (Leuckart, in Sars, 1885) and by Coil & Kuntz (1963) for the related *Syncoelium spathulatum* Coil & Kuntz, 1963.

3. *Terminal genitalia.* The terminal genitalia of the Hemiuroidea show a great number of modifications; but do in fact, with a small number of exceptions, illustrate one basic trend. There are, however, a number of variations in the general pattern, and it is likely that some features of this trend have been evolved independently by parallel evolution. In order to understand both the nature of the trend and the variation, we must first examine the function of these structures. The function of the male terminal genital apparatus is that of ejecting spermatozoa and enabling it to enter the female system, either of another worm or of the same individual. The function of the female terminal genitalia is that of ejecting eggs into the environment, and, we suggest in the case of the Hemiuroidea, receiving spermatozoa from the male terminal genitalia of either another worm or of the same individual. As indicated above, it is clear from our studies of Laurer's canal (Gibson & Bray, 1975) that in the Hemiuroidea, when this duct is present, it functions as a seminal and vitelline drain, not as a vagina (*Trifoliovarium* may be an exception). Evidence from the work of Nollen (1968), who used ³H-thymidine-labelled spermatozoa in *Philophthalmus megalurus* (Cort, 1914) suggests that cross-insemination occurs in the majority of cases whenever possible; but that, when only single worms are present in a host, self-insemination occurs regularly. Nollen also noted that labelled spermatozoa disappeared from the uterine seminal receptacle within fourteen to sixteen days of copulation, which indicates that repeated insemination is required. It would appear, therefore, that self-insemination is a mechanism which has evolved to enable lone specimens in a host to produce fertile eggs. It seems very likely that in some genera self-insemination has become increasingly important, to the extent that the male copulatory apparatus has atrophied. In some cases, such as *Bathycotyle, Gonocerca, Aerobiotrema, Syncoelium* (sensu stricto) and *Tetrochetus*, where the copulatory apparatus has completely disappeared or has been reduced to a vestige, they must, it appears, rely solely upon self-insemination. It is likely that the latter phenomenon has occurred independently in several different groups both within and outside the Hemiuroidea. To illustrate this point, the terminal genitalia and the seminal storage and disposal system of the opecoeline opecoelids are almost identical to those which occur in *Gonocerca*. Too much systematic importance, therefore, should not be placed upon the absence or reduction of the copulatory apparatus.

The main trend in the structure of the terminal genitalia of the Hemiuroidea appears to be as follows. It commences as a simple sinus-organ, produced as a protrusion of the base of the genital atrium, and containing both of the simple, tubular male and female ducts. These ducts come together and unite near the summit of this organ, forming a short hermaphroditic duct which opens via a terminal pore. The close proximity of the male and female ducts which opens into a common genital atrium aids both reciprocal cross-insemination and self-insemination, and, similarly, the development of an hermaphroditic duct further facilitates self-insemination. This latter arrangement (Fig. 8; arrangement A) occurs in the azygiids, where the sinus-organ is a highly contractile, permanent structure, but is usually found in a relatively contracted state. The sinus-organ of the azygiids, which presumably acts as a copulatory organ and possibly aids the extrusion of eggs through the genital pore, is formed from the proximal region of the wall of the genital atrium, and it uses its own intrinsic musculature for extension and contraction. The genital atrium presumably serves as a vagina during copulation, and it is likely that the muscular
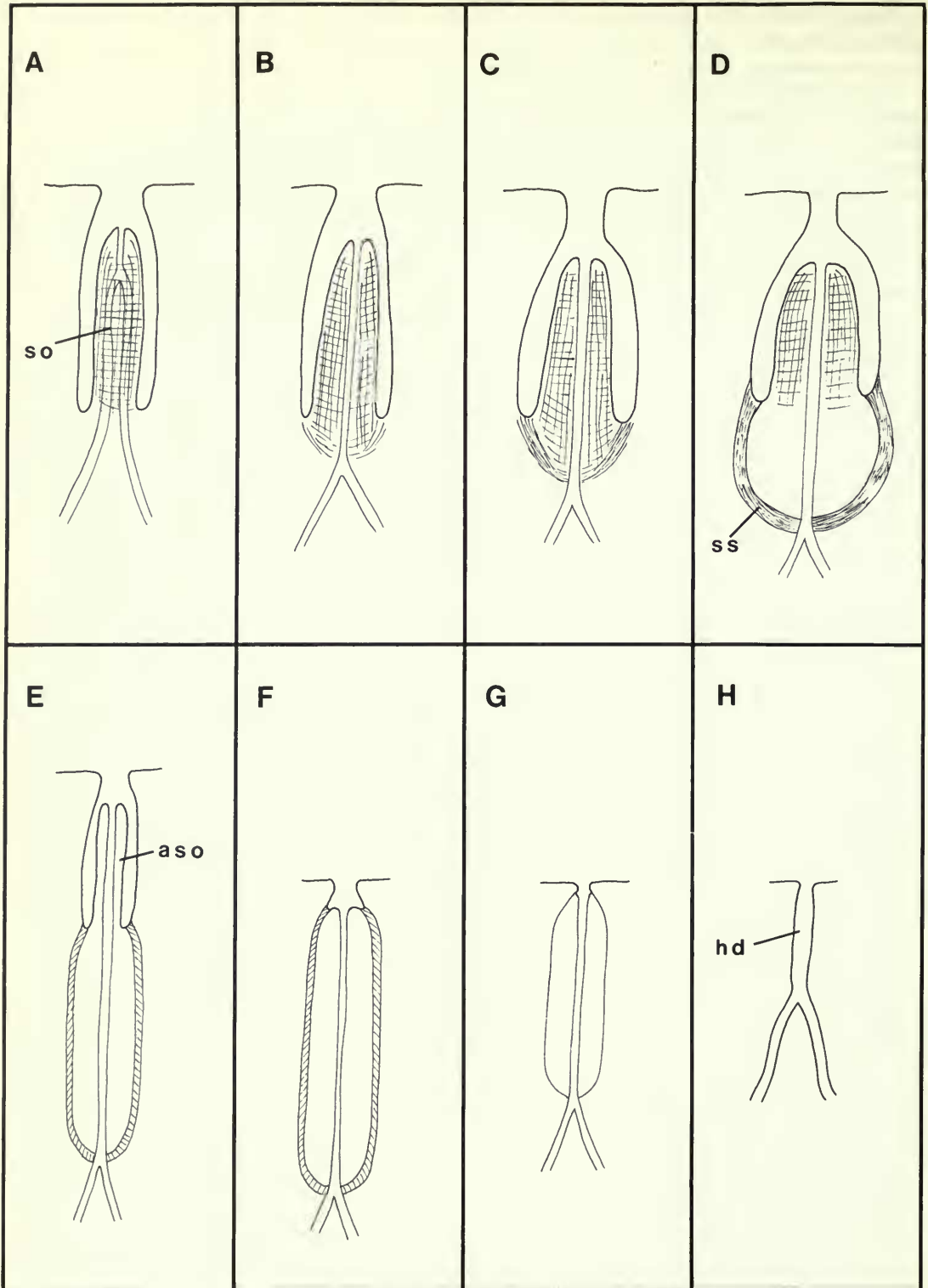
Fig. 8 Different arrangements of the terminal genitalia (see text).
[aso, amuscular sinus-organ; hd, hermaphroditic duct; so, muscular sinus-organ; ss, sinus-sac.]

action of its wall forces the spermatozoa, deposited during copulation, back into the hermaphroditic duct through the aperture of the contracted sinus-organ.

Following on from the type A arrangement, the sinus-organ becomes a relatively larger structure in its contracted state, and some of its intrinsic musculature begins to concentrate into a thin, diffuse sac-like structure surrounding its base (Fig. 8; arrangement B). At the same time, the hermaphroditic duct tends to lengthen, usually reaching at least to the base of the sinus-organ. This arrangement can be seen gradually developing in *Prosorchis*, *Copiatestes*, *Isoparorchis*, *Sclerodistomum*, *Accacoelium* and *Prosogonotrema*, resulting in a type C arrangement (Fig. 8) where the diffuse, muscular thickening at the base of the sinus-organ, which is referred to as the sinus-sac, becomes more apparent in the latter four examples, and, in addition, the intrinsic musculature of the sinus-organ itself tends to become slightly reduced. We consider that the sinus-sac aids the extrusion of the sinus-organ by exerting hydrostatic pressure upon its contents (Gibson & Bray, 1974). Many of the derogenids tend to have an arrangement very similar to that of *Prosogonotrema*, except that the cone-shaped sinus-organ tends to be small. In the dinurine hemiurids the sinus-sac is better developed (Fig. 8; arrangement D), becoming an enlarged oval or tubular structure with a thick, muscular wall, and the sinus-organ is usually cone-shaped, often with a slight reduction in its intrinsic musculature. The sinus-organ may be large, as in *Paradinurus*, or small, as in *Dinurus*, and it should be mentioned that in a small number of dinurines, such as *Stomachicola*, the sinus-organ is absent or reduced to a rudiment: in the latter cases the sinus-sac is also reduced in size. It is noticeable that at about the stage of the type D arrangement, the seminal vesicle, which until now has normally been tubular, tends to become more saccular and often develops sphincters and thus becomes partitioned. These appear to be modifications caused by the fact that, during ejaculation, the spermatozoa now have to be forced into the hermaphroditic duct against the hydrostatic pressure produced when the sinus-sac aids the eversion of sinus-organ. The next stage (Fig. 8; arrangement E) is that the intrinsic musculature of the sinus-organ is then lost, resulting in the fact that it must be entirely everted by hydrostatic pressure. This arrangement can be seen in the Elytrophallinae and in the Glomericirrinae, especially in the former, where the sinus-organ appears to be almost totally amuscular, the sinus-sac is well developed and the seminal vesicle is surrounded by an extremely thick muscular wall. The latter structure is presumably necessary because of an increased hydrostatic pressure necessary to evert the sinus-organ. In the next stage (Fig. 8; arrangement F) the genital atrium is reduced in size and a permanent sinus-organ is lost. The latter is replaced by a short, temporary sinus-organ, rarely seen in fixed specimens, which is formed by evagination of the hermaphroditic duct under hydrostatic pressure. As the hydrostatic pressure is less than that required in the type E arrangement, because of the much smaller sinus-organ and genital atrium, pressure is usually exerted on the seminal vesicle by sphincter muscles or by a thin, muscular layer in its wall, rather than by a thick, muscular wall. This arrangement occurs in the Hemiurinae, Lecithochiriinae, *Stomachicola* and a small number of related dinurines, the Opisthadeninae, the Lecithasterinae and the Quadrifoliovariinae. Finally, in the Hysterolecithinae, Trifoliovariinae, Lethadeninae, Plerurinae, Macradenininae, Dictysarcinae, Prolecithinae and Gonocercinae, the sinus-sac is gradually atrophied (Fig. 8; arrangement G) until in genera such as *Aerobiotrema* and *Gonocerca*, it is lost completely (Fig. 8; arrangement H). Presumably, as mentioned above, in the latter groups the ability to cross-inseminate becomes reduced and is finally lost altogether. It is worth noting that there is a slight deviation within the Hemiuridae, in that the Glomericirrinae, with the type E arrangement, and the Lecithochiriinae, with the type F arrangement, have developed an ejaculatory [prostatic] vesicle. This appears to be a modification of the ejaculatory duct, the function of which is not known for certain. It may, however, form a temporary storage organ as part of a mechanism for ejecting larger quantities of spermatozoa during each ejaculation. If this is true, then the glandular cells, which often line it, may function, with regard to the stored sperm, in the same way that the pars prostatica does to normal quantities of sperm passing through this duct during ejaculation.

One group, the Hirudinellidae, stand out as being totally distinct from the remainder of the hemiuroids in that they possess a 'cirrus-sac'. This structure almost certainly developed independently of the sinus-sac; but it does appear to be analogous. The reason why such a structure

has developed in this group is probably because its ancestors lost, or did not develop, an hermaphroditic duct, with the result that the copulatory organ ('cirrus') did not contain the female duct. In this group, therefore, both the male and the female ducts have developed their own finger-like projections from the wall of the genital atrium. It seems certain that the 'cirrus-sac' of the hirudinellids is not homologous with the cirrus-sac which is found in many other groups of digeneans. At first sight, it is somewhat difficult to see how the hirudinellid arrangement could have evolved from the type A arrangement; but other morphological features of the hirudinellids suggest a relatively close affinity with some of the other 'primitive' hemiuroids. For this reason, it seems unlikely that the hirudinellids split away very early in hemiuroid evolution before the development of an hermaphroditic duct. It is possible, however, to envisage the gradual separation of the male and female ducts of the type A arrangement, where the hermaphroditic duct is short, much in the same way as appears to have occurred in some species of *Halipegus*, where the two ducts open separately at the end of the sinus-organ. It is very unlikely that the Hirudinellidae resemble the ancestral form of the hemiuroids, as it is difficult to imagine how an hermaphroditic duct could have been derived from the hirudinellid arrangement.

We can assume that the presence of apparatus well adapted to enable cross-insemination to occur is the primitive condition in the hemiuroids, as cross-insemination occurs in all other groups of helminths. Even in the primitive hemiuroids, however, it is almost certain that self-insemination does occur, and Dawes (1946) notes that self-insemination of lone specimens of the aspidogastrean *Aspidogaster conchicola* has been observed. It seems likely that the type A arrangement in our trend is primitive. It is a fact that the majority of hemiuroids differ from the majority of helminths in that the copulatory organ is not the usual cirrus, which is often enclosed by a cirrus-sac. Nevertheless, all of the structures termed 'cirrus' are not homologous, as the copulatory organs of many groups of animals have a phallic appearance. In addition, it is unlikely that all of the structures termed 'cirrus-sac' are homologous, as similar 'sacs' surround the base of, and are associated with the protrusion of, many eversible organs, e.g. the proboscis sac of the Acanthocephala. If we examine the aspidogastreans, the majority of species do possess a cirrus-sac, but several do not. There appears to be no evidence in the latter group for the presence of an hermaphroditic duct. As it seems difficult to envisage the development of an hermaphroditic duct, similar to that occurring in the hemiuroids, from a form with a cirrus-sac, it is possible that the rhabdocoel-like ancestors of the digeneans possessed a temporary penis-papilla ('cirrus'), lacking a penis-bulb ('cirrus-sac'), which was formed from the wall of the genital atrium. Commencing with such a structure, it is possible to envisage the development of all of the variations of the terminal genitalia which occur in the Digenea and Aspidogastrea.

A suggested evolutionary scheme within the Hemiuroidea

Published works on evolution within the Digenea are few. Aspects of this subject have been discussed by workers such as Odening (1974), and detailed comments on particular groups have been given by others, such as Bayssade-Dufour & Maillard (1974); but only a few workers, such as Poche (1926) and Cable (1974), appear to have indicated detailed evolutionary relationships within the Digenea as a whole. The majority of evidence in the more recent work has come from larval morphology and details of the life-history. As discussed in our introduction, we believe that much of the evidence based upon such information is questionable. Admittedly data from the intra-molluscan stages are likely to be of some value, but only at the higher taxonomic levels, and, as indicated on p. 38, there are some anomalies. If, as Rohde (1972) suggests, the cercariae were 'invented' by the digenean ancestors as a mechanism to aid the transmission from the molluscan host to the vertebrate host, evidence based upon cercarial morphology, especially as this larval stage is more susceptible to environmental changes than the others, is somewhat dubious. Although the majority of phylogenetic hypotheses on the evolution of and within the Digenea have been based upon larval characteristics, there is evidence that workers are beginning to reappraise the value of adult morphology. Powell & Sogandares-Bernal (1970), for instance, stated: 'While on the subject of larval trematodes, the systematic value of comparative anatomical studies of the terminal genitalia and sensory structures of adult worms should be emphasized.

Homologies and analogies of terminal genitalia (for example in the Hemiuroidea) should prove useful in determining phylogenetic relationships.'

Using evidence outlined in the trends illustrated above, we have attempted to build a hypothetical picture of the evolution of the Hemiuroidea. Our proposed relationships are expressed in Fig. 9. We believe that the most primitive groups are the azygiids and the ptychogonimids, and that the most closely related of these to the ancestors of the remainder of the hemiuroids appear to be the leuceruthrine azygiids. These groups exhibit a combination of primitive characters, such as a follicular vitellarium, a sinus-organ without an accompanying sinus-sac and with Laurer's canal acting as a seminal and vitelline drain. The Leuceruthrinae, which appears to exist as a single species, possesses the same gonadal arrangement as that which occurs in the vast majority of the remainder of the hemiuroids. Another interesting feature which may indicate primitiveness in this group is that in known azygiid life-cycles the cercariae are eaten directly by the definitive host. This suggests the possibility that the azygiids evolved before the acquisition of the second intermediate host which occurs in most digenean life-cycles. Other primitive groups are the Hirudinellidae, Bathycotylidae, Isoparorchiidae, Syncoeliidae, Accacoeliidae and Sclerodistomoididae, and it seems likely that they, especially the latter four, have arisen from a common ancestor. Nevertheless, there are features of the syncoeliids, such as the presence of seven vitelline lobes in the syncoeliines, which suggest that they are more advanced than indicated by the position which we have allocated to them in our 'evolutionary picture'; but, as discussed above (p. 126), these anomalies can be explained. In the latter groups a sinus-sac develops (a 'cirrus-sac' in the case of the hirudinellids) and the vitellarium becomes tubular. In our opinion the remainder of the hemiuroids have evolved from an ancestor resembling the present-day sclerodistomids, although most probably lacking Manter's organ and with more posteriorly situated gonads. From this ancestral form, which presumably possessed a vitellarium consisting of seven tubules, a well-developed sinus-organ and sinus-sac, and Laurer's canal (which although opening dorsally was on the point of evolving a rudimentary Juel's organ), four main lines appear to have evolved. These are: (1) the modern members of the Sclerodistomidae; (2) the Derogenidae; (3) the Lecithasteridae, Dictysarcidae and the Didymozooidea (see p. 133); and (4) the Hemiuridae and Bunocotylidae. The development of Juel's organ, in the rudimentary and or the fully developed form, has occurred in all of these groups. As forms with Laurer's canal opening dorsally also occur in three of the groups, it seems more likely that Juel's organ has arisen independently by parallel evolution than by the concurrent evolution of forms with and without this organ in all of these three groups.

The sclerodistomids are the only one of these groups which either have not developed a complete Juel's organ or in which no members of the group possessing such an organ survive, although rudimentary forms occur in *Prosogonotrema* and *Prosorchis*. It would appear that despite the position of the gonads, the prosogonotrematine and prosorchiine genera are perhaps more closely related to the other three groups outlined above than the sclerodistomines.

The Derogenidae are a very successful group with a complex mixture of primitive and advanced features, especially with regard to the nature of the seminal storage and disposal apparatus in the female reproductive system. Nevertheless, the majority of members tend to be relatively similar in gross morphology, although it seems likely that the three subfamilies of this group separated quite early in the evolution of the group. They probably owe their success to the fact that they tend to fill niches where competition is somewhat reduced, i.e. the stomach of oceanic fishes, in the case of the Gonocercinae and the Derogeninae, and both the stomach of brackish water and freshwater fishes and the mouth and eustachian tubes of amphibians, in the case of the Halipeginae.

The Lecithasteridae appear to have evolved via forms similar to *Trifoliovarium*, but still retaining a uterine seminal receptacle and a rudimentary seminal receptacle. From this form developed the modern members of the Trifoliovariinae and, after the independent formation of Juel's organ, the Hysterolecithinae. The remainder of the lecithasterids could have evolved from forms similar to *Trifoliovarium* by the loss of Laurer's canal, much in the same way as *Cladolecithotrema* has probably developed; but it seems more likely that they have evolved from hysterolecithine ancestors. This is suggested by the great morphological similarity between the
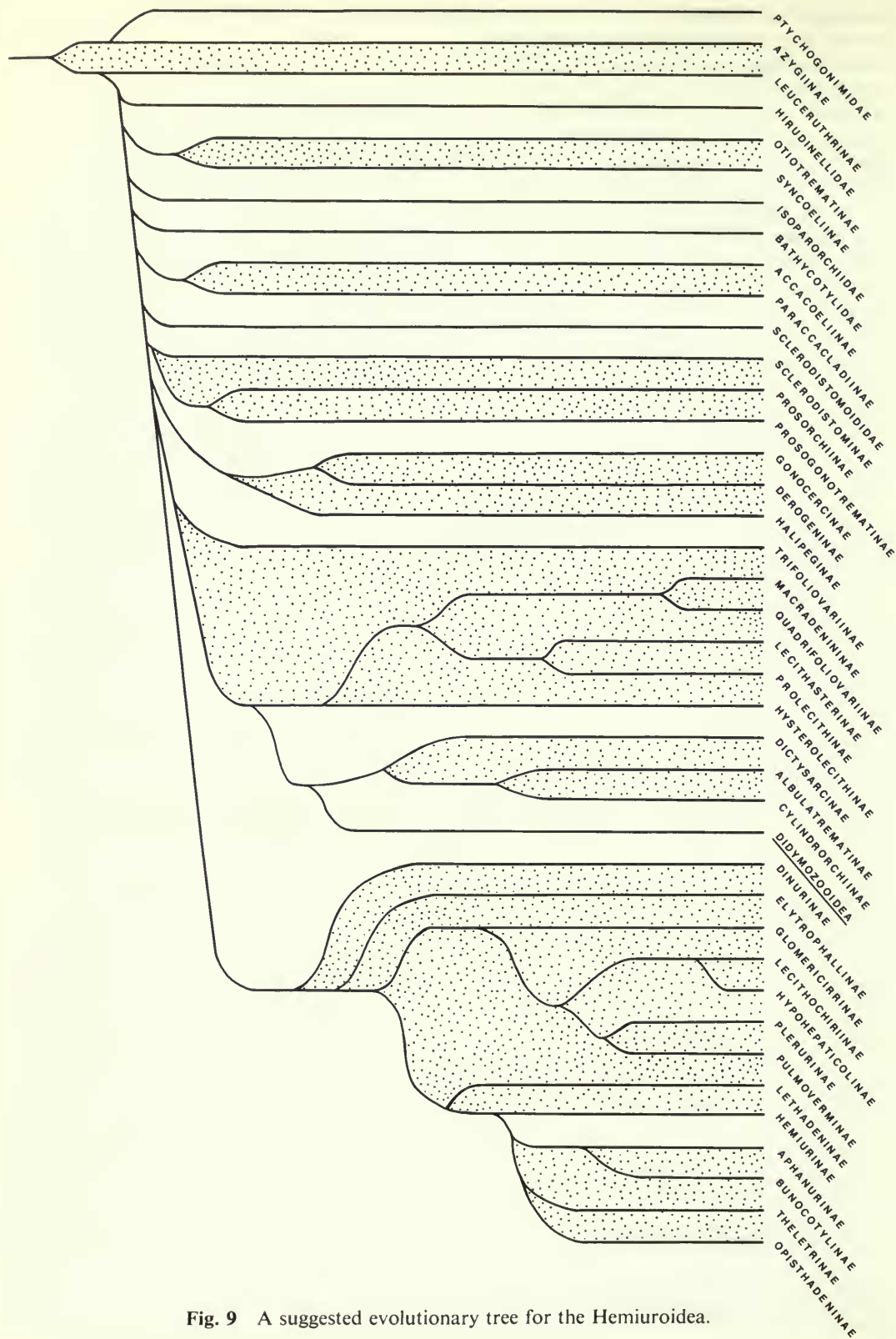
Fig. 9 A suggested evolutionary tree for the Hemiuroidea.

Hysterolecithinae and some of the other lecithasterids and because the thick-walled nature of the blind seminal receptacle in the rest of the lecithasterids suggests that it might have evolved from Juel's organ by hypertrophy of the 'inner vesicle'. It is also apparent, because of the presence of Juel's organ and other morphological similarities, that not only the Dictysarcidae, but also the Didymozooidea (see below), may have evolved from hysterolecithine ancestors.

In the largest group, the Hemiuridae, an ecsoma in association with a plicated tegument appears to have developed (see p. 41), although the former is occasionally reduced and the latter is often completely lost. These adaptations appear to be associated with the hostile habitat of the majority of hemiurids, the stomach of marine teleosts which is a region of variable pH and osmolarity. The most primitive group appears to be the Dinurinae, some of which have features in common with some of the modern sclerodistomids, although all appear to possess a fully developed Juel's organ. The dinurines probably gave rise to the elytrophallines by the development of an amuscular sinus-organ and associated changes in the seminal vesicle. The elytrophallines could then have given rise to: (1) the Glomericirrinae, by the development of an ejaculatory (prostatic) vesicle, which in turn gave rise to forms, such as the Lecithochiriinae, by the loss of a permanent sinus-organ; and (2) the Hemiurinae and the Lethadeninae, by the loss of a permanent sinus-organ. The Bunocotylidae appear to have evolved from ancestral hemiurines by the loss of the ecsoma. It is worth noting that some members of the Aphanurinae still retain a plicated tegument. In the members of the Bunocotylinae, which are extremely small, Juel's organ appears to have been lost, there apparently being no obvious mechanism for disposing of excess seminal and vitelline material. It is possible that these compact and apparently advanced worms utilize not only space, but also spermatozoa and vitelline material, more efficiently, thus reducing the value such a specialized organ. In the opisthadenines Juel's organ appears to have developed into a blind seminal receptacle, much in the same way as we suggest it developed in the majority of the lecithasterids.

Throughout the evolution of this group it is clear that there is a general decrease in body-size, ranging from the giant azygiids and hirudinellids to the minute bunocotylids. Associated with this decrease in size is a more efficient utilization of body-space, such as the development of a compact vitellarium, and a more efficient utilization of excess reproductive products. In addition, although less certain, there appears to be an increase in the proportion of the body occupied by the uterus, and an increase in the dependency upon self-fertilization, thus reducing the need for large and complex terminal genitalia.

Some comments on the relationship of the Didymozooidea and the Paramphistomoidea to the Hemiuroidea

The Didymozooidea are a group which several early workers, such as Odhner (1907) and Poche (1926), considered to be evolved from hemiuroid stock. This early work was based upon adult morphology. Baer & Joyeux (1961), however, basing their hypothesis on the work of Ishii (1935) which indicated that adults of this group developed directly from eggs, recognized the Didymozoidea as a new subclass, distinct from the Digenea, within the class Trematoda. Recently Cable (1955, 1974), using evidence from larval stages, has reiterated Odhner's initial hypothesis that this group is derived from hemiuroid stock. Skrjabin (1955) and Yamaguti (1971) present the didymozooids as a distinct suborder and superfamily, respectively, to the hemiuroids, but do not comment on any relationship between the two.

If those didymozooid genera with a simpler and more conventional morphology, such as *Nematobothrium* van Beneden, 1858,* are examined, several similarities with the hemiuroids are apparent. The testes are normally pre-ovarian and the ovary normally occurs anterior to the vitellarium. The male and female terminal ducts fuse, often forming a short hermaphroditic duct, and open via a common genital pore, and in some instances a small terminal papilla not unlike a sinus-organ is present. In addition, the shape and arrangement of the gonads in juvenile specimens of *Didymocystis acanthocybii* Yamaguti, 1938 (as figured by Yamaguti, 1970), are very

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* The conception of the genus used here is that of Yamaguti (1971).

similar to those of the dictysarcid hemiuroid *Elongoparorchis*. More convincing, however, are the facts that a uterine seminal receptacle is present in *Nematobothrium robustum* Yamaguti, 1970, and that Odhner (1907) has described what appears to be a well-developed Juel's organ in the closely related *N. scombri* (Taschenburg, 1879) (Fig. 10A). Although the latter structure in *Nematobothrium* spp. has usually been referred to as a seminal receptacle, Yamaguti (1970), when describing *Neonematobothrioides poonui*, noted that it contained germ-cells and vitelline material, in addition to spermatozoa. An apparent Juel's organ was also seen by Dollfus (1935) in *Nematobothrium pelamydis* (Taschenburg, 1879). Juel's organ of the didymozooids appears to differ slightly from that in the hemiurids, for example, in that the 'inner vesicle' is not completely enclosed proximally by the outer region of the organ, suggesting that it is perhaps slightly more primitive (see p. 121). The presence of Juel's organ and a uterine seminal receptacle, however, does not appear to be the usual condition in the more highly developed didymozooids. In the majority of these cases the uterine seminal receptacle has apparently been lost and Juel's organ appears to have become transformed into a blind seminal receptacle, which is connected to the oviduct by a short duct, much in the same way as blind seminal receptacles have probably been formed in the majority of lecithasterids and the opisthadenine bunocotylids. In sections of an unidentified didymozooine [close to *Didymocystis* Ariola, 1902] from *Katsuwonus pelamys* off Papua New Guinea, the outer half of the blind seminal receptacle has a thick wall, possibly being the vestige of the outer region of Juel's organ, and the inner half (that closest to the duct) of this seminal receptacle has a thin wall, possibly being formed from the part of the 'inner vesicle' not enclosed by the outer region of Juel's organ (Fig. 10B).

These observations on the gross morphology and on the nature of the seminal storage and disposal apparatus in the proximal female reproductive system of certain didymozooids suggest to us that this group did evolve from hemiuroid stock close to the origins of the Dictysarcidae probably from an ancestral form of hysterolecithine lecithasterid (see Fig. 9).
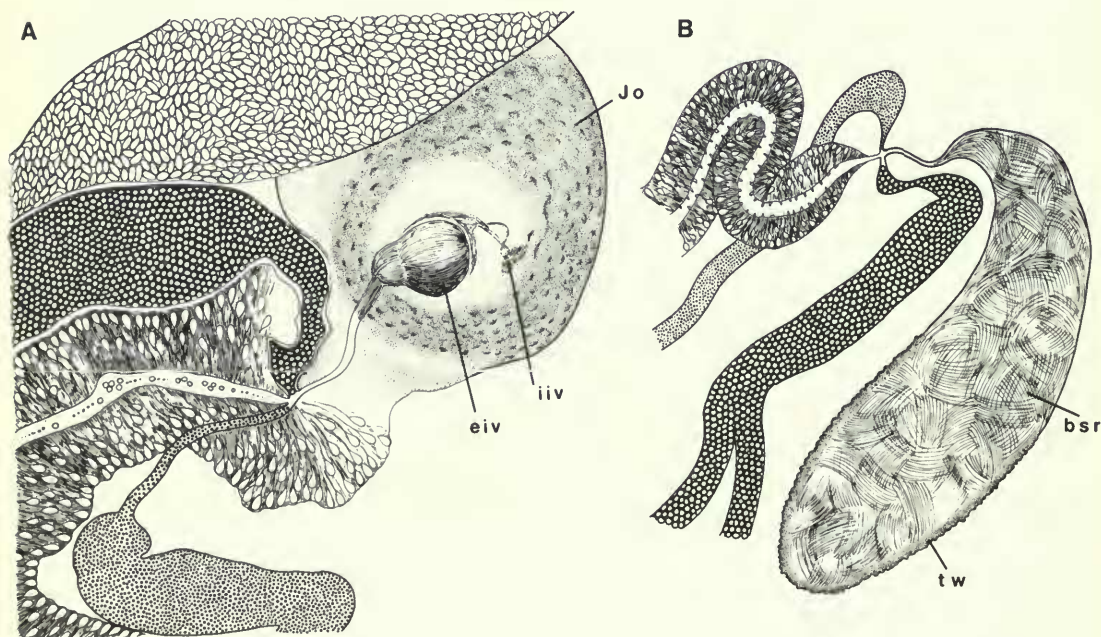

Fig. 10 Parts of the seminal storage and disposal apparatus in the female reproduction system of two didymozooids: A. *Nematobothrium scombri* (modified after Odhner, 1907); B. Unidentified didymozooine. [bsr, blind seminal receptacle; eiv, external 'inner vesicle'; iiv, internal 'inner vesicle'; Jo, Juel's organ; tw, thick-walled region of blind seminal receptacle.]

It is also worth noting that there are certain morphological features which suggest that there may be affinities between the paramphistomoids and some of the more primitive hemiuroids. These include a follicular vitellarium, the absence of a prepharynx, paired testes which are usually pre-ovarian, the presence of Laurer's canal in association with a uterine seminal receptacle and similar terminal genital apparatus. The paramphistomoids differ fundamentally in adult morphology only in the fact that the excretory pore is dorsal rather than being terminal. Although the hindbody is almost absent in this group, there is also a tendency for its reduction in certain hemiuroids, especially in the Sclerodistomidae. The paramphistomoids are generally considered to be stomach parasites of terrestrial vertebrates: several genera have, however, been recorded from teleosts. One particular group, the Brumptiidae Stunkard, 1925, appears to be morphologically very similar to the hemiuroids in that its members possess a well-developed sinus-sac and an hermaphroditic duct, and, in the lateral fields, there is a distinct hindbody present in the form of lobes, being somewhat similar to, but smaller than, those which occur in the syncoeliid *Otiotrema*.

Although workers such as Dawes (1936) have considered the paramphistomoids to be very primitive, Cable (1974) places this group well up one of the branches of his evolutionary tree. He also places it on quite a distinct branch to the hemiuroids, although Poche (1926) had placed them much closer together. Evidence from adult morphology suggests that the paramphistomoids might have been derived from hemiuroid stock close to the point where the syncoeliids and hirudinellids evolved. Nevertheless, there does appear to be fundamental differences in the morphology of the larval stages and the life-history which tend to preclude any serious consideration of this relationship until the significance of these differences is fully understood.

Acknowledgements

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